NEW YORK FISH AND GAME JOURNAL

VOLUME 10 JANUARY, 1963 NUMBER 1

ECOLOGY AND MANAGEMENT OF LARGEMOUTH BASS AND BLUEGILLS IN FARM PONDS IN NEW YORK[1]

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ABSTRACT

To construct a factual and reasoned basis for a fish-stocking and management policy applicable to farm ponds in New York, various species and species combinations were studied. This paper concerns largemouth bass (*Micropterus salmoides*) and bluegills (*Lepomis macrochirus*) stocked according to three different formulae. Data on survival, growth, reproduction, standing crops, harvests, and population condition were summarized and compared. Pond-owner preferences and practices, and pond costs, were determined.

It was concluded that a bass-bluegill combination might prove satisfactory in: (1) larger, deeper New York ponds whose surface temperatures rise above 80° F. for several weeks each summer; (2) ponds where weeds can be controlled; (3) ponds whose owners have a genuine interest in fishing and managing the pond for bluegills as well as bass. A majority of farm ponds in New York likely do not meet these criteria.

About 20,000 farm ponds had been constructed in New York by 1962. Most were built with advice and aid from the U. S. Soil Conservation Service. The first year in which many ponds (over 500) were built under its direction in New York was 1947.

Many of these ponds were stocked with fish. Stocking and management recommendations based on regional studies were not available before 1960. The ponds were usually stocked more or less in accord with recommendations developed farther south. The stocking formula

[1] Derived from a Ph.D. thesis submitted to the Graduate School at Cornell University in 1961. This study is a contribution of Federal Aid in Fish and Wildlife Restoration Project F-17-R. Additional funds were received from the New York State Conservation Council and from the U. S. Department of Agriculture. Data were collected by Cornell graduate assistants S. B. Saila, W. H. Wolfrum, E. P. Snyder, R. W. Wahl, and H. A. Regier, all under the direction first of Dr. D. A. Webster and later Dr. A. W. Eipper. Each contributed labor, insights and suggestions. Much of the value of this study is due to Dr. Eipper's direction, aid and encouragement. Other members of the Cornell faculty, particularly Profs. H. B. Brumsted, C. A. Carlozzi, L. S. Hamilton, D. S. Robson, and G. A. Swanson, gave valuable advice. Many graduate and undergraduate students assisted, especially R. V. Miller. Criticism was received from more than twenty biologists familiar with farm-pond problems, including P. F. Allan of the Soil Conservation Service. D. M. Payne helped with diagrams, C. W. Lyon helped with design and construction of sampling gear, and Mrs. A. Klock typed manuscripts. The pond owners cheerfully granted use of their ponds.

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often used was 100 largemouth bass fingerlings and 1,000 bluegill fingerlings per acre, stocked during the same summer. Frequently fish of other species entered or were added by the owner. Fish populations in many ponds were soon in unsatisfactory condition according to Saila (1950) and Wolfrum (1953).

Investigations on farm-pond fish populations began at Cornell in 1949. A short-term investigational approach was used for the first few years due to uncertainty of research funds. With financial support from the Federal Aid in Fish and Wildlife Restoration program, a longer-term experimental approach became possible in cooperation with the State Conservation Department.

Early in these investigations it was learned that some deeper or spring-fed ponds remained cool enough to support trout satisfactorily (Eipper, 1960). Thus in 1950 the pond investigations were separated into two major studies; one involved brook trout, brown trout and rainbow trout in the cooler ponds and the other involved bass, sunfish, catfish, etc. in warmer ponds. Emphasis in the warm-water studies was placed on the largemouth bass-bluegill combination, with less emphasis on largemouth bass-golden shiners, and channel catfish. These were chosen either because they were popular locally or had been recommended by biologists from other regions.

The basic objective was to construct a factual and reasoned basis for a fish-stocking policy and management methods applicable to farm ponds in New York. The studies on warm-water ponds managed for fishing are described in the present paper and in two papers to appear in the next issue of this Journal (i.e., Regier 1963a; 1963b). Similar studies on bait-fish ponds have been discussed by Forney (1957a), and results of studies on cold-water ponds by Eipper (1960). The three papers based on the warm-water studies concern, respectively, largemouth bass (*Micropterus salmoides*) and bluegills (*Lepomis macrochirus*), largemouth bass and golden shiners (*Notemigonus crysoleucas*), and channel catfish (*Ictalurus punctatus*).

The general introduction given here and the general methods section that follows apply to all three warm-water studies. A more detailed discussion of methods and materials used for bass and bluegills follows the general methods section in the present paper. Details on methods used for the other species combinations are given in the respective papers. This method of presentation was chosen to include all important procedures, but not to overload each of the papers with those common to all.

GENERAL METHODS

Fish populations in ponds are influenced directly or indirectly by six broad factors: geographic location; construction features of ponds; pond-owner characteristics; fish-stocking formulae; fertility, fertilization,

and weed control; and nature of harvests. Following are short discussions of these as well as of types of data collected, methods of collecting them, and their general reliability.

Project Area

Ecological relationships within a pond are affected by its general geographic location. More specifically the climate, topography, soils, and types of agriculture in the watershed area each exert some influence on the dynamics of a pond's fish population.

Forty-nine ponds were used in the warm-water studies. All but one were within 25 miles of Ithaca. The climate and geography of the area as these affect ponds do not differ markedly from other areas in the State except the Adirondack and Catskill Mountains.

Almost all project ponds lay in New York's plateau region which Nobe, Hardy and Gratto (1958) described from an agricultural viewpoint as follows:

1. Topography is limiting on the hills, favorable in the valleys.
2. Climate is generally favorable only to forage production.
3. Hill soils are generally acid, of low fertility, and have poor water-handling capacity; valley soils are gravelly, acid, and responsive.
4. Dairy farming predominates, other types locally important.

The average growing season is between 140 and 160 days (Frederick, Johnson and MacDonald, 1959), compared with 100 to 120 days in the Adirondacks and Catskills and 180 days near Buffalo and Rochester.

Experimental Ponds

Table 1 shows the number of ponds used for each warm-water category. These ponds were not random samples of farm ponds in the project area. Rather, they were chosen on the basis of their accessibility, their adaptability to seining, and the cooperativeness of the pond owner. The author judges that they were typical of the better-managed two-thirds of the ponds in the project area.

Of the 49 ponds, 11 were on Cornell University lands, 6 were on lands controlled by other institutions or government agencies, and the remaining 32 were privately owned.

The main uses of a pond usually have some effect on its fish population. The privately-owned ponds were commonly used in several of the following ways: recreation (fishing, swimming, skating, scenery), stock water, fire protection, domestic water supply, irrigation, and general "conservation". Over-all importance of individual pond uses in New York is approximately in the order of listing, though the first three may be interchanged. Of the 11 Cornell ponds, nine were constructed primarily for experimentation with fish.

Table 1. Number of Ponds and Stocking Rates Used in the Three Phases of the Study of Warm-water Farm Ponds

Species combination	Stocking rate *	Number of ponds	Studies began §	Studies ceased
Largemouth bass-bluegills	100:500 simultaneous	9	1953–1954	1960
	100:1,000 simultaneous	8	1953–1954	1960
	100:1,000 staggered	10	1953–1955	1960
Largemouth bass-golden shiners	100:400 simultaneous	10	1954–1957	1961
Channel catfish	variable	12	1952–1955	1960

* "Simultaneous" means both species were stocked as fingerlings during the same calendar year; "staggered" means fingerling bass were stocked about one year before fingerling bluegills.
§ Work on different ponds began in different years.

Almost all project ponds were constructed under the supervision of either SCS technicians or agricultural engineers. Ponds near Ithaca are usually between 0.2 and 0.5 acre in size with a maximum depth in late summer of between 5 and 10 feet. They are usually built on gentle slopes or in shallow valleys draining 5 to 10 acres. A large horseshoe-shaped dike is typical.

Few ponds used in the warm-water experiments had strong springs, though some probably received considerable inflow from subsurface seepage. Four Cornell ponds received water from a creek, and two others received inflow from field tiles. Forney (1957b) described the chemical characteristics of ponds in the project area.

About one-quarter of the ponds had no trickle tube or one that became nonfunctional shortly after construction. All, except the four Cornell ponds with controlled inflow, had grassed spillways. Nine of the 49 ponds were poorly planned or poorly constructed, with serious leaking due to poor seal the most frequent fault.

Almost all ponds had the recommended steep banks to a depth of 3 feet or more from high water level. Many had fairly extensive areas less than 3 feet deep during late summer periods of low water.

During the first few years of its existence, a pond passes through a form of ecological succession, i.e., a primary hydrarch successional development. Normally the older ponds are more suitable habitats for fish than very new ponds. Project experiments were begun in ponds that were usually 1 or 2 years old, and no ponds were older than 5 years at experimental stocking.

POND STOCKING

Each of the following factors associated with pond stocking likely has some effect on subsequent population dynamics: stocking rate (number per acre) of each species, stocking ratio (number of one species relative to another), source of stock (strain of fish), size of stock, and date of stocking. The last three were uncontrolled in these experiments since project personnel accepted hatchery stock where and when it was available.

Corrective stocking, as an attempt to change an unsatisfactory population condition, was not used in these studies except in one case.

FERTILIZATION

Pond owners in most southern states are urged to use commercial fertilizer to increase and stabilize a pond's carrying capacity and to control weeds. When project experiments with bass and bluegills were designed, it was hoped that all the ponds would be properly fertilized. Fertilization was not emphasized in the plans for bass-shiner and catfish studies.

Private cooperators in the bass-bluegill experiments were given instructions on how to fertilize and were urged to follow them. All, without exception, failed to follow through consistently. Most private ponds received fertilizer several times during the first summer after stocking, once or twice the next summer, and little thereafter.

Ponds on Cornell lands were fertilized approximately according to plan until 1958 when most fertilization was discontinued.

Thus fertilization as a factor affecting fish population dynamics was not controlled in this study. But the ponds can be separated into heavily fertilized and lightly fertilized groups. The breakdown of the control on fertilization was not without advantage since project ponds as a result were more typical of the majority of farm ponds in New York.

WEEDS AND THEIR CONTROL

Weeds become a problem in many New York ponds. Common weeds include the filamentous algae *Cladophora*, *Spirogyra*, and *Chara*, and rooted aquatics such as *Potamogeton*, *Typha*, and *Myriophyllum*.

Project ponds usually became weedy within a few years after construction. Heavily fertilized ponds were often partially covered in summer with mats of *Cladophora;* poorly fertilized ponds were particularly subject to infestation with *Chara*, *Typha*, and *Potamogeton*.

Cooperators occasionally attempted weed control. Project personnel seined the ponds each year and this required that they be relatively weed-free. Almost all project ponds received chemical weed treatments at least once, made according to recommendations by Eipper and Brumsted (1958). Most received a number of treatments; one received 14 in 6 years. No fish kills were observed following any of these.

Angling and Fish Harvests

Cooperators were advised at the outset of experiments not to harvest a species until the fish had reproduced successfully. Also angling records were to be maintained. Cooperators adhered to these rules quite closely but it was found impossible to control unauthorized fishing in several ponds.

Project personnel did not recommend catch quotas for individual ponds except during 1958 and 1959. Cooperators' harvests were generally light. Project personnel occasionally removed stunted fish from some ponds in an attempt to improve population conditions.

Annual Inventories

Project personnel inventoried the experimental ponds annually. Data collected yielded estimates of growth and survival of the original stock, occurrence and relative success of reproduction, and standing crops of each species by a number of size strata.

The population of each species in a pond was stratified by length into "large", "intermediate", and "small" fish. Strata limits are defined for different species in the relevant papers of this study. Petersen estimates were made of the population of large and intermediate fish of each species, and samples of fish in these strata were measured. Relative abundance of small and young-of-the-year fish of each species was estimated.

Inventory equipment was changed somewhat during the investigations as inventory methods evolved. In 1952 the following seines were used: 150-foot, 1-inch cotton bag seine 12 feet deep in center; 60-foot, $\frac{3}{8}$-inch cotton bag seine 7 feet deep in center; and 10-foot, $\frac{1}{8}$-inch "common sense" minnow seine. Seines available in 1956 were: 150-foot, $\frac{3}{4}$-inch cotton bag seine 8 feet deep in center; 75-foot, $\frac{1}{4}$-inch nylon bag seine 8 feet deep in center; and 15-foot braided minnow seine. Seines used in 1958 were: 150-foot, $\frac{3}{4}$-inch nylon bag seine 10 feet deep in center; 75-foot, $\frac{1}{4}$-inch nylon bag seine 8 feet deep in center; and 10-foot, $\frac{1}{8}$-inch knitted nylon minnow seine. All mesh sizes are given in terms of bar measure. Other equipment included four or more live cars, scales, measuring boards, data forms, waders, etc.

Inventories during and after 1958 were more comprehensive than in preceding years. Before 1958, inventories were made typically as follows. Project personnel made two visits to the pond about 3 days apart during the summer. During the first visit the population was sampled with a bag seine of a size judged to be most suitable to the pond area; e.g., a $\frac{1}{4}$-acre pond was seined with a 75-foot seine, a $\frac{3}{4}$-acre pond with a 150-foot seine. The fish captured were separated by species and size strata, and the small fish were returned to the pond immediately.

Those of each species in each of the large and intermediate strata were counted, marked by clipping a corner of the caudal fin and released. During the second visit the numbers of marked and unmarked fish in each species stratum were determined. A sample of fish in each species stratum was chosen, and the individual fish were weighed and measured. Scales were occasionally taken to check ages. Inventories were conducted as rapidly as possible to minimize adverse effects on the fish.

In 1958 and thereafter, inventories were made in autumn to increase their efficiency and reduce adverse effects on the fish. Most ponds were at least partly drained to facilitate seining, and some were completely drained. Petersen estimates were made where complete censuses were not possible. All or a large random sample of the fish captured during the first visit were marked, measured, and released. During the second visit all or a large random sample of the fish captured were examined for marks and were measured. The number of fish in each of the three size strata was estimated as illustrated in Figure 1.

The length frequency distribution of all bass captured was divided by inspection into arbitrary strata and Petersen estimates were then made for each stratum. The arbitrary strata usually coincided with natural size-class groupings. In order to get estimates by standard strata an estimate by arbitrary strata may have to be partitioned. Thus in Figure 1 one arbitrary stratum with an estimate of 91 bass extends from 8 to 12 inches. But 9.95 inches is the dividing line between two standard strata, i.e., between harvestable and subharvestable. The estimate of 91 bass was partitioned in proportion to the fraction of all bass captured in this arbitrary stratum that were subharvestable (i.e., 60/82) or harvestable (i.e., 22/82).

Estimates of the standing crop by species and by standard strata were derived from the Petersen estimates, length frequency distribution of all fish captured, and the length-weight relationship. The length frequency relationship was used to estimate the mean weight of fish within each 0.1-inch substratum. The total number of fish captured in each 0.1-inch substratum was then multiplied by the corresponding mean weight to estimate the total weight of bass captured in each substratum. These substrata totals were then summed by arbitrary strata within standard strata. These sums were then individually multipled by their "Petersen factor" (i.e., total estimated number in stratum/total number captured in stratum) and summed within standard strata to give estimates of the standing crop by species by standard strata. The extra computational work required in making such estimates was offset by less work in the field and greater precision of estimates.

Minnow seines were used in all years to check for reproduction. Usually the relative abundance of small and young-of-the-year fish was estimated during July or August. During the 1958 inventories, almost

all the young fish in some of the drained and partially drained ponds were captured, separated by species and weighed in aggregate.

Successive years' inventory statistics were compared for each experimental population, taking into account fish harvested or reported dead.

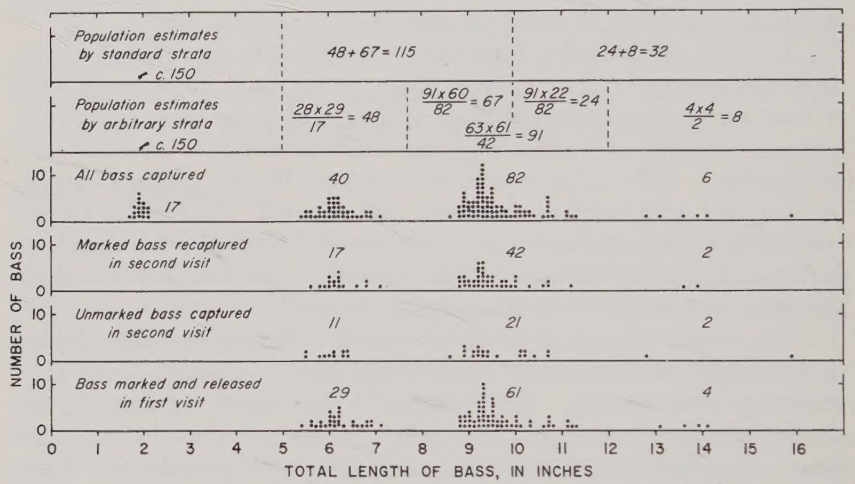


Figure 1. Inventory records and computations showing how length-frequency data were used, after 1957, to estimate number in population by size strata. "All bass captured" refers to all bass captured during the first visit and all unmarked bass captured during the second, plus a sample of small fish captured while minnow seining.

Statistics were adjusted just enough to give reasonable estimates where inconsistencies occurred, e.g., more originally-stocked bass were estimated to be present in Year $X+1$ than in Year X. Selfconsistency was considered worth the price of some loss in objectivity. Further reference is made to these adjustments in the section on survival.

POND MANAGEMENT RECORDS

Records of the following management practices were maintained fairly consistently for most project ponds: fishing effort and catch (date and time spent; length, weight and species harvested), fertilization (date applied, type and quantity), and weed control (date, type).

Cooperators received record booklets with instructions shortly after their ponds were stocked. By 1957 their response to requests for records was quite erratic. Thereafter project personnel made special efforts to obtain the required data. Mailed questionnaires, telephone calls and personal interviews contributed useful information in almost all cases, though these data were not as accurate as would have been desirable.

GENERAL RELIABILITY OF DATA

General methods have been described, and specific details are given in subsequent sections. This section contains a brief discussion of the general reliability of the data collected.

Two or more ponds were dropped from study within a year or two of stocking with each of the species combinations. The reasons included severe fish kills, pond failure, and severe contamination with other species. Few usable data on population dynamics were available for such ponds, but they are included in the following sections to indicate the uncertainties that face both pond populations and the biologists planning to experiment with them.

Inventory data were examined critically to evaluate their reliability. Summer population estimates generally appeared quite reliable during the first two years after stocking. Thereafter summer inventories tended to become less reliable. With the change to autumn inventories the results appeared quite reliable in all cases and highly reliable in most cases.

A number of factors operated to make some 1956 and 1957 summer inventories fairly unreliable. Originally-stocked fish were large and difficult to catch. As the ponds aged, they contained progressively more fish or more year classes. Inventories took longer and mortality resulted, especially in hot weather, either through suffocation or disease. Ponds tended to become weedy and muck was deposited on the bottom. Both processes interfered with efficient seining, and in such circumstances project personnel often had to use the smaller bag seines where the 150-foot seine, if usable, would have provided more reliable samples.

Factors which contributed to increased efficiency in autumn inventories were as follows. Wherever possible, ponds were drained or partially drained (or pumped out), and a total census was attempted. Even in ponds that could not be drained, the water level tended to be lower than in midsummer and the ponds were usually less weedy. Most ponds were seined when water temperatures were between 38° and 55° F.; at these temperatures warm-water species are less active and easier to capture by seining. Fish could be held in live cars for considerable periods at the lower temperatures with less danger of serious mortality. The 150-foot bag seine used in 1958 and thereafter was 2 feet deeper in the center than the 150-foot seine used in preceding years. This large seine was used even in small ponds. Finally, a more complete series of data was collected during the autumn inventories of 1958 and thereafter than in the summer inventories of preceding years.

Though some inventory data from 1956 and 1957 were not very reliable, these weaknesses were partly offset by increased efforts in 1958 to obtain management and harvest records for those years.

The number of individual fish, per species per stratum, that were weighed and measured was small before 1957, usually only 10. This

sample size was increased to 20 in 1957. In the autumn inventories of 1958 and subsequent years as many fish as possible were measured, and a subsample was weighed. These increases in sample size were found necessary due to the increased number of age groups present in each pond. Also more precise estimates of standing crops within species strata were desired.

Relative success of reproduction was estimated usually on the basis of the abundance of fry or fingerlings in summer seining, and sometimes from the size of that year class in subsequent years. Such data measure both reproductive success as such and survival of young to the time of sampling. Since these data were not very precise it was decided to summarize reproductive success in terms of four arbitrary classes (see section on reproduction following).

Reliability of management records has been mentioned. Records were usually neither as comprehensive nor precise as they might have been. But the information was useful in analyzing pond population dynamics and also in analyzing pond-owner preferences and practices.

In summary, the data are somewhat less reliable than had been hoped, but are believed to be considerably more reliable than is usual in fishery statistics. The author has made a special effort constantly to bear in mind the relative reliability of the data in all the discussion that follows.

LARGEMOUTH BASS AND BLUEGILL STUDY

Warm-water ponds in New York became eligible for free bass and bluegill stock from government agencies about 1945. Saila (1950) examined 13 New York bass-bluegill ponds in 1949 and considered eight unsuccessful; Wolfrum (1953) examined 26 such ponds from 1951 to 1953 and found 14 in unsatisfactory condition. In both cases, some of the unsatisfactory as well as some of the satisfactory ponds had been contaminated with other fish species. Though these findings and those of other workers (Regier, 1962c) tended to be discouraging, ponds continued to be stocked with bass[3] and bluegills. During the period 1950 to 1958, soil conservation districts aided in constructing about 8,300 ponds in New York of which almost half were stocked with bass and bluegills, and most of the remainder with trout.

These studies were designed primarily to determine if a simple change in stocking policy from the one used would result in greater success with bass and bluegills in New York ponds. An important second objective was to obtain information on the ecology of these species in small ponds.

[3] "Bass", as used in this study, refers to largemouth bass.

MATERIALS AND METHODS

The general methods used throughout the studies of warm-water farm ponds have been presented. The materials and methods that pertained more directly to the work on bass and bluegills are described under the following topics.

Experimental Bass-Bluegill Categories

It is generally held that stocking rates and ratios exert an important effect on population condition in a pond at least for several years after stocking. Based on studies in different states, quite a number of stocking formulae have been devised some of which were summarized by Lagler (1952). On the assumption that the stocking formula has an important effect, project personnel decided to test three. These were:

100 bass and 500 bluegills, simultaneous;
100 bass and 1,000 bluegills, simultaneous;
100 bass and 1,000 bluegills, staggered.

Fingerlings were used; with "simultaneous" stocking both species were introduced during the same summer, with "staggered" stocking bluegills were introduced the year following bass. Stocking was usually done in late summer.

Experimental Ponds

General characteristics of project ponds are described in a preceding section. Table 2 contains more detailed information on bass-bluegill ponds.

Ponds that were improperly designed or constructed have been identified in Table 2. Experiments in some of the ponds were terminated before 1960 for reasons given in the footnotes. Eight of the 27 experimental pond studies were discontinued within 5 years. This represents an attrition rate of about 30 per cent.

In Kentucky, Hall (1959) found an attrition rate of about 65 percent over a period of about 5 years. In Alabama (Moss and Hester, 1956) the rate was about 30 per cent over 4 years, if improperly stocked ponds are left out of consideration. These findings suggest that if an experimenter using privately-owned ponds desires a given number of replicates for a 5-year study, then he should begin with about twice that many.

Ponds were assigned to experimental categories so that size frequency distribution of pond areas was similar in the three categories (Table 2).

Stocking Data

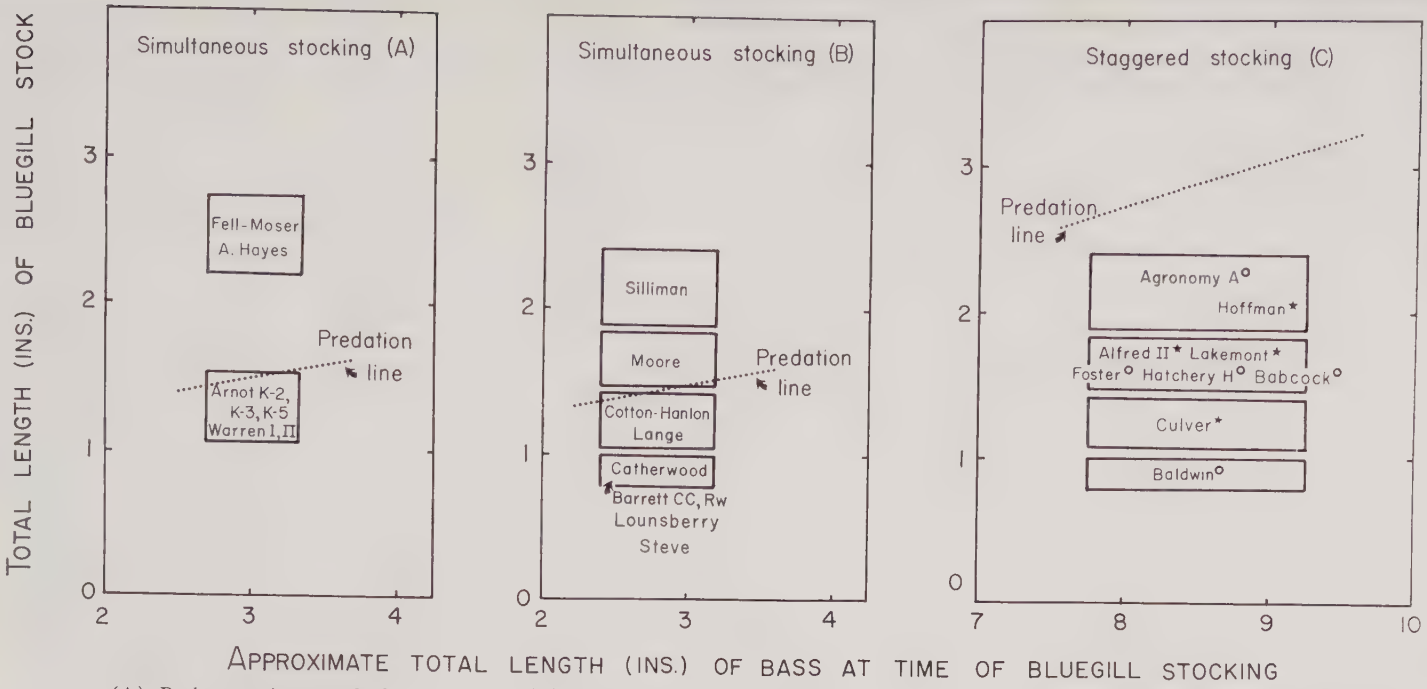
The experiments were not all begun in the same year. Stock used in different years was not quite the same size and was from different

Table 2. Characteristics of Project Ponds Stocked with Bass and Bluegills; Ponds within Categories Ranked in Order of Mean Surface Area

Pond	Mean area (acres)	Age of pond at stocking (years)	Period studied	Footnote remarks
Experimental category : 100-500 simultaneous				
Arnot K-3	0.17	4	1953–1960	
Arnot K-1	0.18	1	1950–1952	b, j
A. Hayes	0.23	0	1953–1960	l
Barrett CC	0.30	0	1954–1960	a
Moore	0.31	0	1954–1960	b
Steve	0.33	1	1954–1955	a, g
Lounsberry	0.44	3	1954–1956	a, f
Fell-Moser	0.45	2	1953–1958	d
Cotton-Hanlon	1.28	1	1954–1960	
Experimental category : 100-1,000 simultaneous				
Arnot K-2	0.20	4	1953–1960	a
Lange	0.25	1	1954–1960	a, b
Arnot K-5	0.30	4	1953–1959	i
Barrett Rw	0.31	0	1954–1960	a
Silliman	0.32	0	1954–1958	j
Warren I	0.52	3	1953–1960	c, l
Catherwood	0.80	1	1954–1960	c
Warren II	0.82	1	1953–1960	
Experimental category : 100-1,000 staggered				
Beattie	0.26	1	1954–1960	a
Hatchery H	0.27	3	1952–1960	b
Baldwin	0.34	1	1953–1960	
Lakemont	0.34	0	1953–1960	a, b, l
Culver	0.36	1	1953–1955	e
Hoffman	0.38	1	1954–1960	
Babcock	0.45	4	1954–1960	e
Alfred II	0.61	1	1953–1958	k
Agronomy A	0.65	1	1953–1959	h, l
Foster	0.82	0	1953–1960	c

a. Pond improperly designed or improperly constructed.
b. Pond overstocked, see text.
c. Pond understocked, see text.
d. Fish suffered severe winterkill, experiment discontinued.
e. Fish suffered severe summerkill, experiment discontinued.
f. Pond became almost dry due to leak, experiment discontinued.
g. Dike failed due to large watershed, experiment discontinued.
h. Pond drained to repair leak, experiment discontinued.
i. Pond drained to begin another experiment.
j. Pond seriously contaminated with other fish species, experiment discontinued.
k. Pond too far from Ithaca, experiment discontinued.
l. Fish suffered moderately severe summerkills, but experiments continued.

sources and hence of different genetic origin. Figure 2 shows the range in total length of bluegills at the time of stocking, and the approximate



(A) Both species stocked in October 1953.

(B) Bass stocked in July and bluegills in September 1954.

(C) * Denotes bass stocked in October 1953 and bluegills in September 1954.
° Denotes bass stocked in July 1954 and bluegills in September 1955.

Figure 2. Size ranges for bass and bluegills at time of stocking in the various ponds studied. The "predation line" is discussed under "bluegill mortality and bass predation" (p. —).

range in total length of bass at the time of bluegill stocking. Approximate stocking dates are given.

The number of fish stocked in a particular pond was based on areas estimated before stocking. Areas were determined by plane table surveys except in a few cases where they were estimated visually. Ponds were resurveyed in 1958 and 1959, and estimates were made of the mean area during the growing season. The revised mean areas differed in some cases from the first estimates[4]; thus some ponds had been overstocked, and others understocked. Three ponds were understocked by more than 10 per cent: Warren I pond by about 40 per cent, Catherwood and Foster ponds by 20 per cent each. Five ponds were overstocked: Moore pond by 50 per cent, Lange pond by 40 per cent, Arnot K-1 and Hatchery H ponds by 30 per cent, and Lakemont pond by 20 per cent. The stocking "errors" made in project ponds were likely well within the range of errors made in stocking non-project ponds in New York generally. In this study, "incorrectly" stocked ponds were considered as typical ponds in their respective categories unless stated otherwise.

Source of stock for the ponds changed from year to year and included hatcheries in Pennsylvania, Massachusetts and New York, as well as ponds near Ithaca (N. Y.). Samples of stock received from 1952 to 1954 were weighed and measured, but such data were not available for the 1955 stock. Regier (1959) found evidence that bluegills stocked in the Beattie, Hoffman, and Lakemont ponds in 1955 were stunted yearlings.

Bluegill stock was stratified by size but bass were not (Figure 2). Bluegills were stratified in order to determine whether smaller stock could reproduce as early as larger stock. Project personnel stocked all the experimental ponds and took precautions to ensure that the stock entered the ponds in good condition.

Data Collection

Data were recorded on population size, growth, reproduction, harvest, fish kills, pond fertilization, weed control, etc. General methods have been described, but further details of the inventory methods used need to be included.

In the bass-bluegill ponds, population estimates were made each year until 1958. Reproduction checks were continued in most ponds until 1960.

It was planned to estimate the standing crop of a species in a pond by three size strata: large, intermediate, and small. For various reasons the limits between these strata changed somewhat from year to year. In

[4] The "errors" in area estimation may have arisen as a combination of several factors: prestocking survey at time of high or low water, mistakes in surveying, changes in pond area over the years.

order to make such data (i.e., standing crops within various species strata) comparable from year to year, the data had to be adjusted to give estimates in terms of some standard strata. The following strata limits were chosen as standard, in terms of total length in inches:

Largemouth bass		
Harvestable	Large	greater than 10.0
Subharvestable	Intermediate	5.0 to 10.0
	Small	less than 5.0
Bluegills		
Harvestable	Large	greater than 6.5
Subharvestable	Large	5.2 to 6.5
	Intermediate	3.0 to 5.2
	Small	less than 3.0

Subsequently a dichotomous classification was superimposed on the trichotomous classification and resulted in splitting the bluegill "large" stratum. The bases for the harvestable and subharvestable limits are discussed in the section on harvests.

The method used in adjusting inventory data to give estimates of standing crops by standard strata may be illustrated by an example. In the 1955 inventory of the Baldwin pond, the population estimate of "large" bass (over 9.4 inches long) was 32. Ten "large" bass had been measured and of these only one was smaller than 10.0 inches. Thus it was estimated that three of the 32 (estimated) bass were subharvestable, i.e., intermediates with respect to standard strata limits. When estimates of within-strata populations had been adjusted it was necessary to recalculate the means for length and weight. This usually required further stratification since the data falling into standard strata might no longer be random samples of strata populations.

Did such adjustments introduce much subjectivity into the data? The data from most inventories required little or no adjustment, but in some cases moderate adjustments were necessary. Objectivity lost was considered to have been more than offset by comparability gained.

RESULTS

Growth, reproduction and yield are major considerations in evaluating the success of a farm pond fish population. The data obtained in the present study for the ponds stocked with bass and bluegills are analyzed under these and related topics.

Survival of Original Stock

Project experiments were designed to provide data on the following questions concerning survival of original stock:

1. What are typical survival rates for bass and bluegills at the stocking rates and ratios used? Are differences significant?
2. If small enough, does bluegill stock suffer predation from larger bass stock?
3. Is survival of bass and bluegill stocks within ponds correlated?

Information on these questions is presented following a discussion of methods used in obtaining and comparing survival data.

Survival data for original stock were derived from annual inventory figures. Original stock was identifiable in the field in all ponds until 1957. In 1958 scale samples were taken to aid in identifying year classes. Scales of original stock usually have features that distinguish them from subsequent year classes (Regier, 1962b). The author therefore considers that identification of original stock was highly reliable in all inventories.

A number of uncontrolled factors complicated the analysis of survival; the more important of these were:

1. Ponds were stocked on different dates in different years.
2. Populations were inventoried on different dates.
3. Some population estimates were not very reliable.
4. The number of fish harvested varied, between ponds and years.
5. Some accidental fish kills occurred.

Some adjustments were necessary to render data comparable. To make adjustments involved assumptions; the following assumptions were chosen:

1. Between dates of reliable inventories, the natural mortality rate, $\frac{dN}{dt}$, was at all times proportional to the number present in the population, i.e., $\frac{dN}{dt} = -qN$ where q is the coefficient of natural mortality.
2. The coefficient of fishing mortality, p, was zero when the pond was not being fished, and was either constant and finite during the fishing season, or almost infinitely large over a very short period. This may be restated $\frac{dN}{dt} = -(p+q)N$ where p may be zero, finite, or infinite in different periods of the year, but is constant within those periods.
3. The coefficient of natural mortality did not vary with the source of stock or with the year in which stocking was done.

The above "model" is a simple elaboration of one commonly used in fisheries studies (e.g., Ricker (1958) refers to the coefficients as "instantaneous rates"). This model and the basis for the discussion that follows are presented in some detail by Regier (1962a).

The following methods were used to standardize data for direct

graphical comparison. The adjustments were made in two steps; first on a within-pond basis, and then on a within-category basis.

Figure 3 illustrates the within-pond adjustment for bass stock in the Hoffman pond. The continuous line in Figure 3a estimates the number of original bass present in the pond on any date between July 30, 1954 and October 8, 1958. This "population line" was estimated by methods described by Regier (1962a) from the following data:

Bass stocked on July 30, 1954		38
Estimated survivors on August 9, 1955		21
Number removed in July 1956	6	
Estimated survivors on August 1, 1956		(20)
Number removed in June 1957	5	
Estimated survivors on June 11, 1957		6
Number removed in July 1958	3	
Estimated survivors on October 8, 1958		1

The 1956 population estimate is unreliable since it was based on the re-

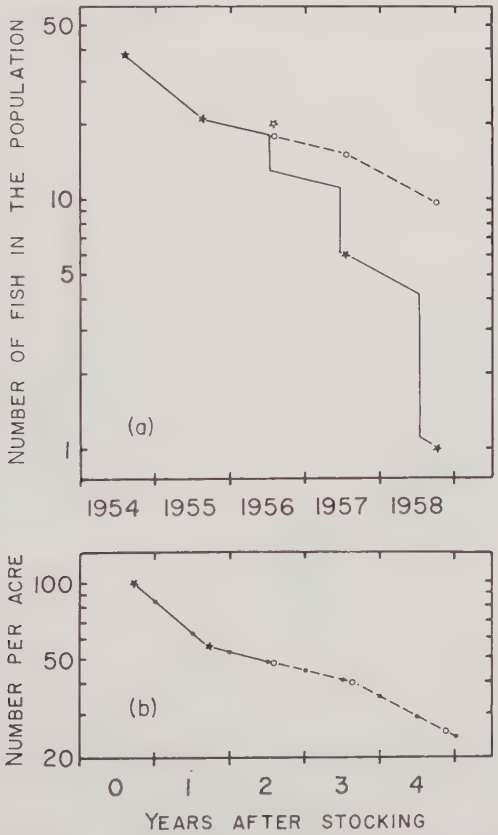


Figure 3. Method of estimating within-population survival in the absence of fishing.

capture of only one marked fish; it was ignored in the analysis. The 1955 and 1957 estimates were accepted as reliable and a constant coefficient of natural mortality was assumed for the intervening period.

The dashed line in Figure 3a is an estimate of the population line that would have existed had there been no fishing. After July 1956, the segments of the dashed line are drawn parallel to corresponding segments of the continuous line on the assumption that the coefficient of natural mortality was unaffected by the fishing mortality.

Figure 3b shows three more steps in standardizing data from individual ponds. The estimated population line has been shifted both with respect to the horizontal and vertical axes. Horizontally the entire line has been moved slightly to the right so that the starting date falls on September 12, the approximate mean data of bass stocking in the project ponds. The vertical axis now denotes the number of survivors per surface acre. Finally, the beads inserted along the line in Figure 3b indicate the estimated number of survivors per acre, in the absence of fishing, on January 1 and July 1 of successive calendar years following stocking.

The January 1 and July 1 estimates of populations in the same category were plotted and adjusted further on a within-category level as illustrated in Figure 4. Here Figure 4a shows estimated survival, in the absence of fishing, for bluegill stock in the 100-1,000 staggered category. Only those data considered quite reliable are included. The first segment of the figure extends from the stocking date to July 1 of

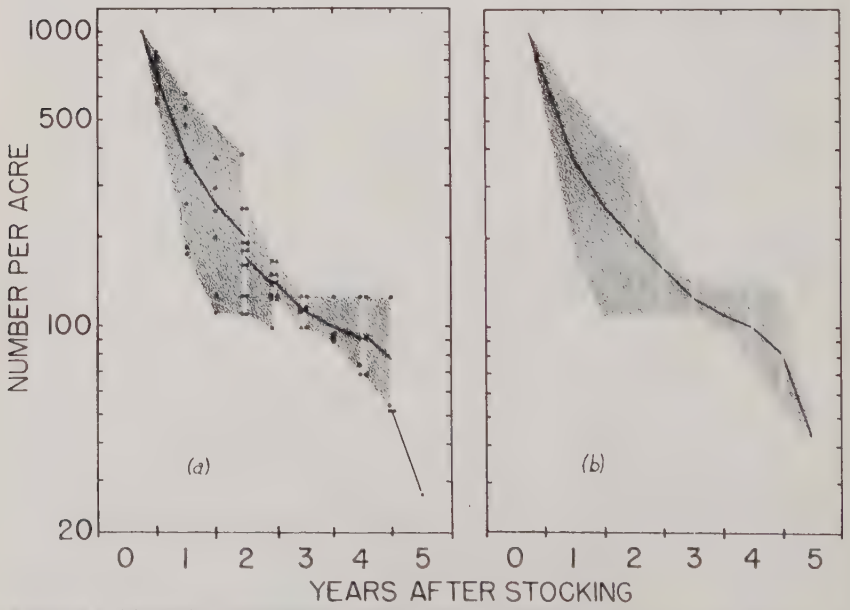


Figure 4. Method of estimating within-category mean survival in the absence of fishing.

Year 2. Reliable survival data for this period were available from seven populations; the first segment is a plot of these data with a line joining their arithmetic means. During the period from July 1 of Year 2 to January 1 of Year 3 only six sets of reliable data were available; the data and means have been plotted in the second segment. The remaining data and means were plotted in a similar manner.

Data means in the various segments of Figure 4a were aligned as shown in Figure 4b. The second segment was raised until the means of data for July 1 of Year 2 coincided in both segments; then the third segment was adjusted so that means for January 1 of Year 3 coincided, and so on.

These segments may be adjusted by actually cutting the figure into segments and rearranging them holding the first fixed; the resulting figure may then be traced onto another sheet of graph paper. Alternatively, the individual estimates plotted in the segment may be adjusted by the factor formed when the mean of data for July 1 of Year 2 in the first segment is divided by that in the second segment. The resulting values, except those for the initial date of each segment other than the first, are then plotted as in Figure 4b. The slope of the line joining the means in Figure 4b is an estimate of the natural mortality coefficient. The adjustments are applications of the assumption that the mortality coefficient was constant for the arithmetic mean of category data, in the same way as was done for individual populations in Figure 3.

The vertical range of the shaded area in Figure 4a represents the observed range in estimated survivors (in the absence of fishing) in different ponds of the staggered category. However, the shaded area in Figure 4b no longer represents the observed range, but rather the relative range, i.e.: (actual range) $\times$ (adjusted mean) $\div$ (actual mean). This, too, is consistent with the assumption of a constant coefficient of natural mortality.

Survival data included in Figure 4, and similar data summaries for other categories and species, were only those considered quite reliable. If two successive estimates of survivors were obviously unreliable, then these and subsequent estimates were not included in the summary except where other evidence (harvest, observed kills, etc.) indicated quite reliably how large the population must have been on respective inventory dates. Furthermore, survival data following severe summerkills or winterkills were not included.

The author, therefore, considers that the data on which Figures 5 and 7 are based are quite reliable and that the assumptions necessary to render the data comparable are quite realistic. However, the summaries contain only data from populations which had not suffered severe kills.

Survival of Bass Stock Figure 5 contains summaries of esti-

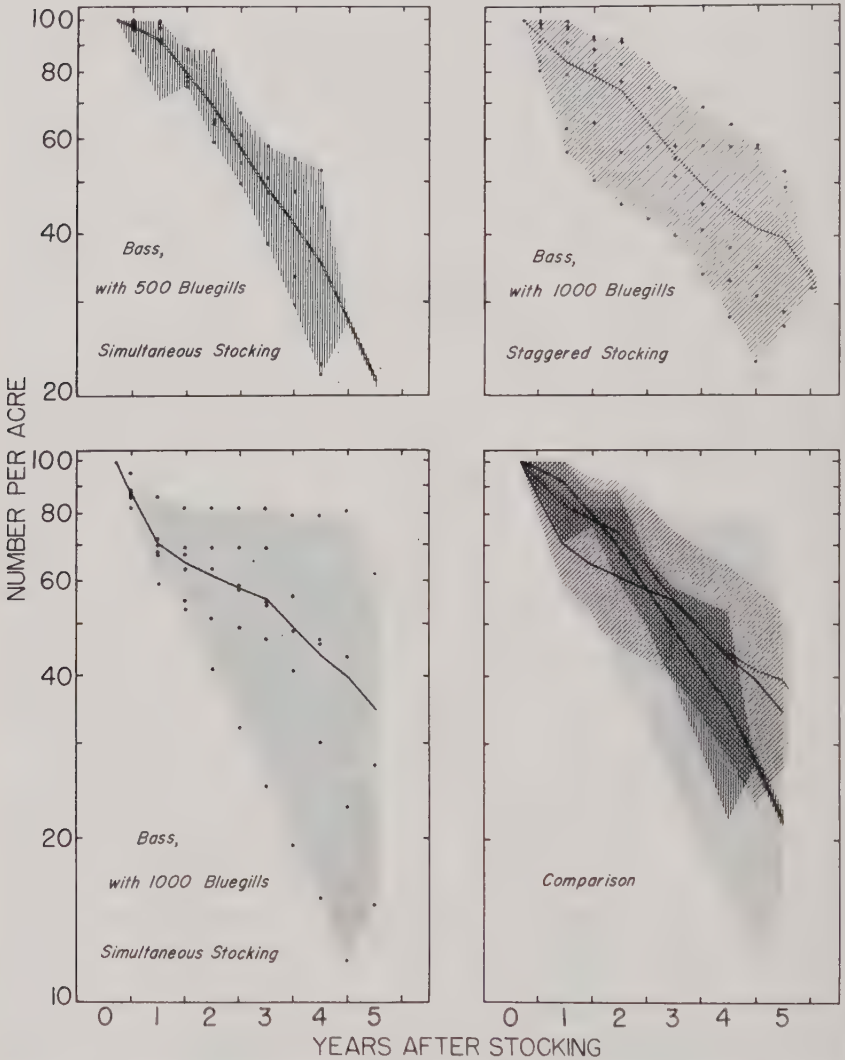


Figure 5. Summary and comparison of survival, in the absence of fishing, for the original bass stock in three experimental categories.

mated survivors of the original bass stock in three experimental bass-bluegill categories. Comparison of survival in the three categories indicates that differences were not significant. The evidence indicates, therefore, that the bluegill stocking rates tested (500 and 1,000 per acre) had little effect on bass survival rates; furthermore, bass survival rates did not differ significantly between the simultaneous and staggered stocking categories.

Since mean survival data were similar in the three categories and

no significant differences were found between categories, the data were pooled to estimate average survival rates for bass; results are shown in Figure 6. The resulting average population line, adjusted to remove the effects of fishing, is approximately straight on the semilogarithmic plot. (Also the average population line in each experimental category was approximately straight.) Unless estimation procedures were biased, the rectilinearity of the line is evidence that the coefficient of natural mortality tended to be constant for bass stock during the first five years following stocking.

It should be noted that the assumption and use of a constant coefficient of natural mortality between times of reliable inventories must have reduced some irregularities in survival. The effect was to smooth data on an annual basis, except where unreliable inventory estimates required the application of this assumption over a 2-year period. Because only the more reliable data were included in the summaries used in Figure 5, unreliable estimates were not common. The author concludes that the bias could not have been pronounced. Curvilinearity in the data for bluegills in the staggered stocking category (Figure 7) and for bass when stocked with golden shiners supports this conclusion.

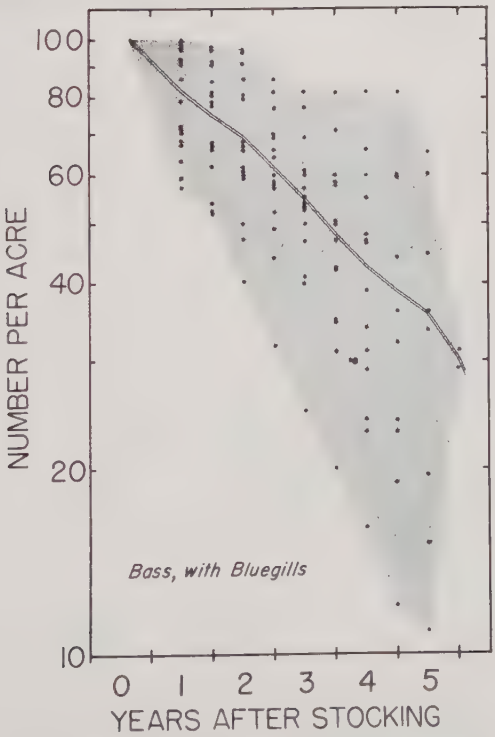


Figure 6. Survival, in the absence of fishing, for the original bass stock in three experimental categories combined.

In order to estimate the average coefficient of natural mortality for bass stock, a straight line was fitted by eye to the data in Figure 6. A restriction was imposed, namely, that the line pass through the point containing stocking information (0.70, 100). The average date of bass stocking was September 12, i.e., at the 0.70 point in Year 0. The estimated line was observed to pass through the point (5.70, 33.8). Now the population model is (Regier, 1962a):

$$N_t = N_0 e^{-q\,(t-t_0)}$$

where q is the coefficient of natural mortality. Then q may be estimated by the method of moments:

$$\text{or} \qquad \begin{aligned} 33.8 &= 100e^{-q\,(5.70-0.70)} \\ e^{-5q} &= 0.338 \end{aligned}$$

From a table of exponential functions it may be determined that

$$\text{and} \qquad \begin{aligned} -5q &= -1.08471 \\ q &= \quad 0.217 \end{aligned}$$

Again from a table of exponential functions it may be determined that, for an average value of $q = 0.217$, the corresponding annual natural mortality rate in the absence of fishing (Ricker, 1958) was about 19.5 per cent.

There is another important point to be made concerning the data summarized in Figure 6. The observed average over 4 years of the annual natural mortality rates ranged from about 5 per cent (Catherwood pond) to 40 per cent (Barrett Rw pond). These extremes were not due to a bias in adjusting data to remove effects of fishing since few bass were removed in the Catherwood pond and apparently none in Barrett Rw pond. Thus the variation in natural mortality rates of largemouth bass was found to be considerable in the ponds studied.

Survival of Bluegill Stock Figure 7 contains graphical summaries of estimated survivors (in the absence of fishing) of bluegill stock in three experimental bass-bluegill categories. These data were estimated by the same methods described for bass. In Figure 8 the graphs for the three categories are superimposed to facilitate visual comparisons.

Numbers of bluegills are shown on the ordinate axes of Figure 7. In each category bass were stocked at 100 per acre. In the simultaneous categories both species were stocked in the same year; in the staggered category bluegills were stocked the year following bass introduction.

Comparison A in Figure 8 indicates that there were significant survival differences between the categories of original bluegill stock (in the absence of fishing) during the first four years after stocking. The significance seems self-evident; hence, no statistical tests were attempted. In particular, bluegills stocked a year after the bass suffered considerably higher mortality than those stocked during the same year. Of the three

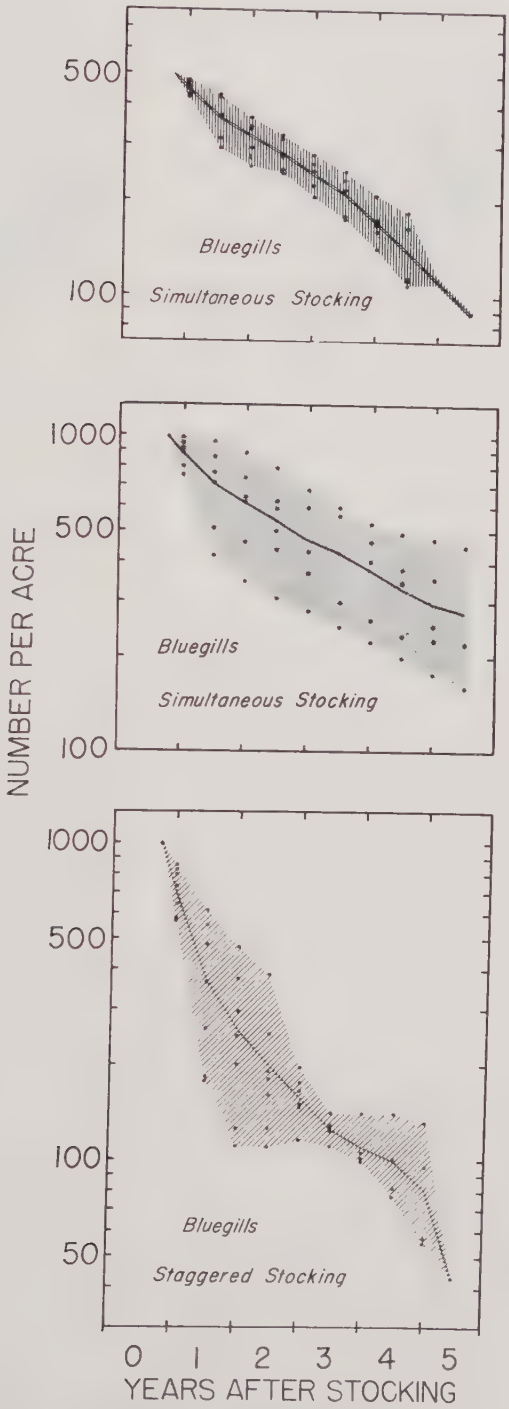


Figure 7. Summary of survival, in the absence of fishing, for the original bluegill stock in three experimental categories.

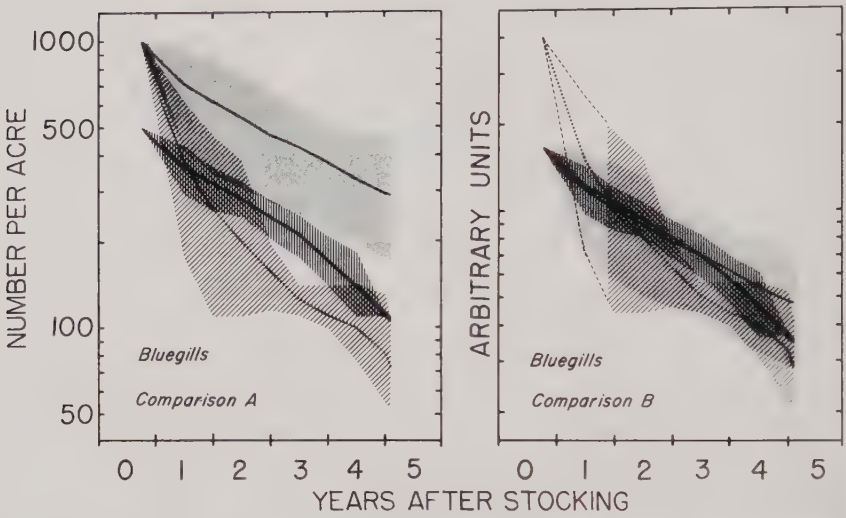


Figure 8. Comparison of survival, in the absence of fishing, for the original bluegill stock in three experimental categories.

categories tested, the largest number of survivors resulted typically when 1,000 bluegills per acre were stocked in the same year as bass. Thus, 3 or 4 years after stocking, an average population of the 100-1,000 simultaneous category contained about twice as many bluegills of original stock as did an average population of the 100-500 simultaneous category, and about three times as many as in the 100-1,000 staggered category. It seems probable that the high mortality of bluegill stock during the first year in staggered populations was due largely to bass predation. In support of this conclusion is the observation that, in ponds where stocking was staggered, bluegill survival improved after the first year, i.e., after the bluegills became large enough to be immune to bass predation.

Comparison B in Figure 8 permits a comparison of natural mortality coefficients (as estimated by slopes of the lines joining means) in bluegill stock of the three categories. Category means and relative ranges from Figure 7 were superimposed, starting with an arbitrary point on the logarithmic scale. The figure includes survival data after the first year for bluegills in staggered populations; the first year's data were deleted since it seemed apparent from Comparison A that the natural mortality coefficient was higher during this period in the staggered populations than in those of the other categories. The data from staggered populations were superimposed on the other data so that the means for survival in staggered and simultaneous populations coincided on January 1 of Year 2. An examination of Comparison B suggests that there were no significant differences in natural mortality coefficients in the data tested. This implies that these coefficients did not vary with the density of the bluegill population within the limits tested. Since this evaluation was partly

subjective (i.e., concerning which data from the staggered category to be deleted), the finding of non-significant differences is inconclusive.

The data used in Comparison B were lumped to estimate over-all average natural mortality coefficients for bluegill stock. Table 3 contains the data on which Comparison B was based, with the arbitrary starting point taken as 1,000, on October 1 of Year 0. (October 1 was the approximate mean stocking date for bluegills in project ponds.) A straight line was fitted by eye to the data and its equation was found to be

$$N_t = N_0 e^{-0.354\ (t-t_0)}$$

The next to the last line in Table 3 shows the estimated survivors (in the absence of fishing) as determined from the straight line. "Goodness-of-fit" may be examined by comparing the last two lines in the table; the author considers the fit to be satisfactory. The close agreement between the data and a straight line implies that the natural mortality coefficient was constant over the years for the bluegill populations tested, i.e., it did not change with the age of the fish or the density of the surviving stock.

A natural mortality coefficient of 0.354 corresponds to an annual natural mortality rate in the absence of fishing of 29.9 per cent.[5] Thus the average annual natural mortality of bluegills stocked in the same year as bass was about 30 per cent. The range of annual natural mortality, averaged over 4 years, in individual populations was about 15 to 35 per cent. Bluegills stocked the year following bass introduction suffered a mortality of about 74 per cent during the first 15 months in the ponds, and thereafter about 30 per cent per year.

Bluegill Mortality and Bass Predation Bluegills stocked in the years 1953 to 1955 were stratified by size before being introduced into the ponds (bass were not). Some ponds contained bass large enough to prey on those bluegills at the time the bluegills were stocked. Did predation occur in some ponds of the simultaneous categories? In the staggered category, did lots of smaller bluegills suffer greater mortality than lots of larger bluegills?

Figure 2 contains bluegill and bass stocking data. Each of its three diagrams contains a "predation line". This line is based on findings of Lawrence (1958) and denotes the maximum size of bluegill that can be swallowed by largemouth bass of a given length. Thus a 3.5-inch bass can just swallow a 1.6-inch bluegill; similarly an 8.5-inch bass can swallow a 2.9-inch bluegill. With respect to possible predator-prey relationships in the ponds stocked simultaneously in 1953 the data show that all but some of the largest bluegills stocked in the Arnot K-2, Arnot K-3,

[5] Data from populations that had suffered severe summerkills or winterkills are not included in Figures 7 and 8 or in Table 3.

Table 3. Estimated Mean Number of Survivors, in the Absence of Fishing, for Bluegill Stock at Semiannual Intervals Following Stocking *

Experimental category	Year 0	Year 1		Year 2		Year 3		Year 4		Year 5	
	Oct. 1	Jan. 1	July 1	Jan. 1	July 1	Jan. 1	July 1	Jan. 1	July 1	Jan. 1	July 1
100-500 simultaneous	1,000 (6)	896 (6)	727 (6)	638 (5)	564 (5)	490 (5)	424 (5)	344 (5)	276 (5)	222 (1)	178 (1)
100-1,000 simultaneous	1,000 (6)	882 (6)	704 (6)	612 (6)	539 (6)	468 (5)	424 (5)	374 (5)	327 (5)	293 (5)	276 (3)
100-1,000 staggered	.. ..	.. ..	.. ..	624 (7)	480 (7)	379 (6)	305 (5)	269 (4)	242 (4)	197 (3)	101 (1)
Mean	1,000 (12)	889 (12)	716 (12)	624 (18)	523 (18)	442 (16)	384 (15)	333 (14)	284 (14)	253 (9)	221 (5)
Estimated survivors §	1,000	917	769	644	540	451	379	317	267	222	186
Deviation in percent †	0	−3	−7	−3	−3	−2	+1	+5	+6	+14	+19

* Means for the data in the 100-500 simultaneous category multiplied by 2 and those for the data in the 100-1,000 staggered category by about 2.5 (see text and Figure 8); figures in parentheses are numbers of populations in each case.
§ Based on straight line fitted to the data (see text).
† Deviation of mean from estimate.

Arnot K-5, Warren I and Warren II ponds could have been swallowed by the bass present; none of the bluegills stocked in the Fell-Moser and A. Hayes ponds could have been swallowed by the largest bass present. The other two diagrams may be interpreted in a similar way. It may be noted that all bluegills were vulnerable in the ponds where stocking was staggered.

The author assumed that the smaller the bluegills were, relative to the bass, at time they were stocked, the more susceptible they were to bass predation, or the longer they could be preyed upon by bass, or both. If this assumption is correct and if predation occurred, it follows that:

1. In the simultaneous categories, fewer bluegills should have survived (say to July 1 of Year 1) in the Barrett CC and Catherwood ponds than in the Fell-Moser, A. Hayes, and Moore ponds.
2. In the staggered categories, bluegills in the Foster, Alfred II and Hatchery H ponds should have suffered more predation than those in the Agronomy or Beattie ponds.

Data to permit tests of these hypotheses are contained in Table 4.

The data consist of the estimated survival of the original stock to July 1 in the year following stocking. Data from the two simultaneous categories were lumped since no significant difference was found between natural mortality coefficients of either bass or bluegills in these categories. The author postulated three grades of possible predation for the simultaneous stocking: none, little, or moderate. For the staggered stocking he considered that predation possibilities were either moderate or marked.

Comparison of the means and ranges in the three groups of ponds where stocking was simultaneous indicates no significant differences in survival. A similar conclusion applies to the two groups of ponds where stocking was staggered. From a consideration of the data in Table 4 and Figure 8 the author infers that bass predation was not important in ponds stocked with bass and bluegill fingerlings during the same year, but that it did occur when bluegill fingerlings were stocked a year after bass.

Comparison of Bass and Bluegill Survival within Ponds Perhaps ponds can be ranked in order of their suitability for fish. It may be that both bass and bluegill survival are similarly affected by such factors as pond size, pond fertility, pond age, and so on. The hypothesis that bass and bluegill mortality rates were correlated within project ponds of the simultaneous categories was tested with Spearman's rank correlation test (Steel and Torrie, 1960). As in previous sections, unreliable data were deleted, as were also data taken following disastrous summerkills or winterkills. The correlation was found to be positive but nonsignificant for each of four sets of data (Regier, 1961).

The evidence indicates, therefore, that little correlation existed between mortality rates of bass and bluegills in ponds stocked during the

Table 4. Degree of Possible Bass Predation on Bluegills *

Marked		Moderate		Little		None	
Pond	Survival §	Pond	Survival §	Pond	Survival §	Pond	Survival §
Simultaneous stocking							
.....	.....	Barrett CC.....	58.2	Cotton-Hanlon.....	62.4	Fell-Moser.....	72.0
.....	.....	Catherwood.....	86.0	Lange.....	76.5	A. Hayes.....	73.0
.....	.....	.....	.....	Arnot K-2.....	96.0	Moore.....	86.0
.....	.....	.....	.....	Arnot K-3.....	84.6	.....	.....
.....	.....	.....	.....	Arnot K-5.....	42.0	.....	.....
.....	.....	.....	.....	Warren I.....	71.0	.....	.....
.....	.....	.....	.....	Warren II.....	51.0	.....	.....
.....	.....	Mean.....	72.1	Mean.....	69.1	Mean.....	77.0
Staggered stocking							
Foster.....	17.7	Agronomy A.....	36.2	.....	.....	.....	.....
Alfred II.....	61.3	Beattie.....	18.4	.....	.....	.....	.....
Hatchery H.....	26.0	.....	.....	.....	.....	.....	.....
Mean.....	35.0	Mean.....	27.3	.....	.....	.....	.....

* Data adjusted to a common stocking date of October 1 in Year 0.
§ In per cent.

same calendar year. The lack of correlation could be taken as evidence that some factors affecting bass and bluegill survival are independent, and that none has an overriding influence.

Growth Rates

Data on growth provided information on several questions. Did the growth rates of the original stock of bass or bluegills, or both, differ significantly in the three experimental categories? Within the population density ranges observed, were growth rates density dependent? How soon after stocking did the original stock attain harvestable size? How soon did the first year class of each species hatched in the pond attain harvestable size? Answers to these questions are prerequisite to sound management recommendations.

Samples of bass and bluegills from each size stratum (i.e., small, intermediate, and large) were weighed and measured. Growth data on original stock were summarized as mean weights within populations at time of inventory. For year classes spawned in ponds, data were estimated mean weights attained at the end of successive growing seasons.

Growth of Stocked Bass Figure 9 shows the within-population mean weights attained by original bass in the three bass-bluegill categories. Category means are also shown and, in the last panel, these have been plotted separately for comparison. The dashed horizontal line at 0.55 pound is the approximate minimum harvestable size, corresponding to 10.0 inches total length.

With regard to Figure 9, two points need emphasis. First, individual points are *means;* thus the scatter of points does not include the total range of weights attained by individual fish. Second, the vertical axis is logarithmic and thus emphasizes relative rather than absolute differences.

Within-category variation was quite pronounced. Thus, 4 years after stocking, the range in mean weights attained by the original bass stock was approximately as follows:

100-500 simultaneous	:	0.5 to 1.9 pounds
100-1,000 simultaneous	:	0.6 to 1.8 pounds
100-1,000 staggered	:	1.0 to 1.9 pounds

The question of whether observed differences were due to density dependent factors is examined in a subsequent section.

Differences between category means were not large when compared with within-category differences. The author considers these differences too small for rejection of the hypothesis of no difference.

In all three categories, some bass in several ponds attained harvestable size in the autumn of the first year following stocking (data not shown). Most bass in most populations became harvestable about midsummer of the second year. In one pond of each of the two simultaneous

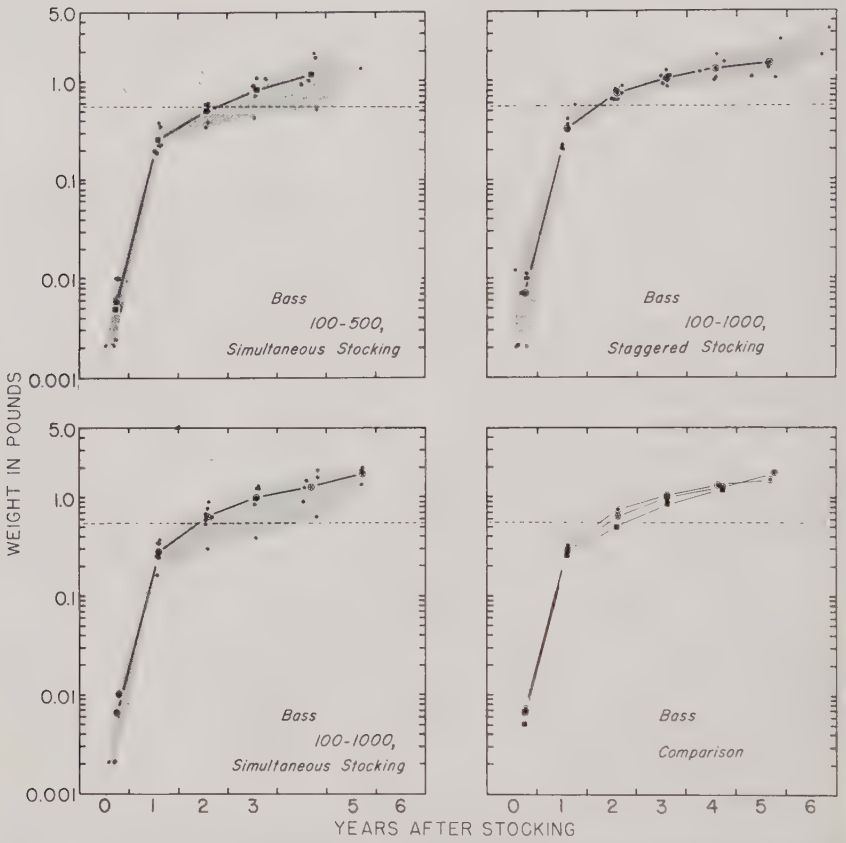


Figure 9. Summary and comparison of growth for the original bass stock in three experimental categories.

categories, most bass did not attain harvestable size until the fourth summer after stocking; presumably this would also occur occasionally in ponds where stocking was staggered.

The largest bass taken in a project pond was 18.0 inches long and weighed 3.6 pounds; it had completed 7 seasons of growth (i.e., age VI+).

Growth of Stocked Bluegills Figure 10 contains summaries of bluegill growth data presented in the same manner as those for bass. The dashed horizontal line is the approximate minimum harvestable size, 0.25 pound at a length of about 6.5 inches.

As with bass, within-category variation was pronounced three years after stocking; the observed ranges among estimated population means within categories were approximately as follows:

100-500 simultaneous	:	0.25 to 0.40 pound
100-1,000 simultaneous	:	0.20 to 0.45 pound
100-1,000 staggered	:	0.35 to 0.55 pound

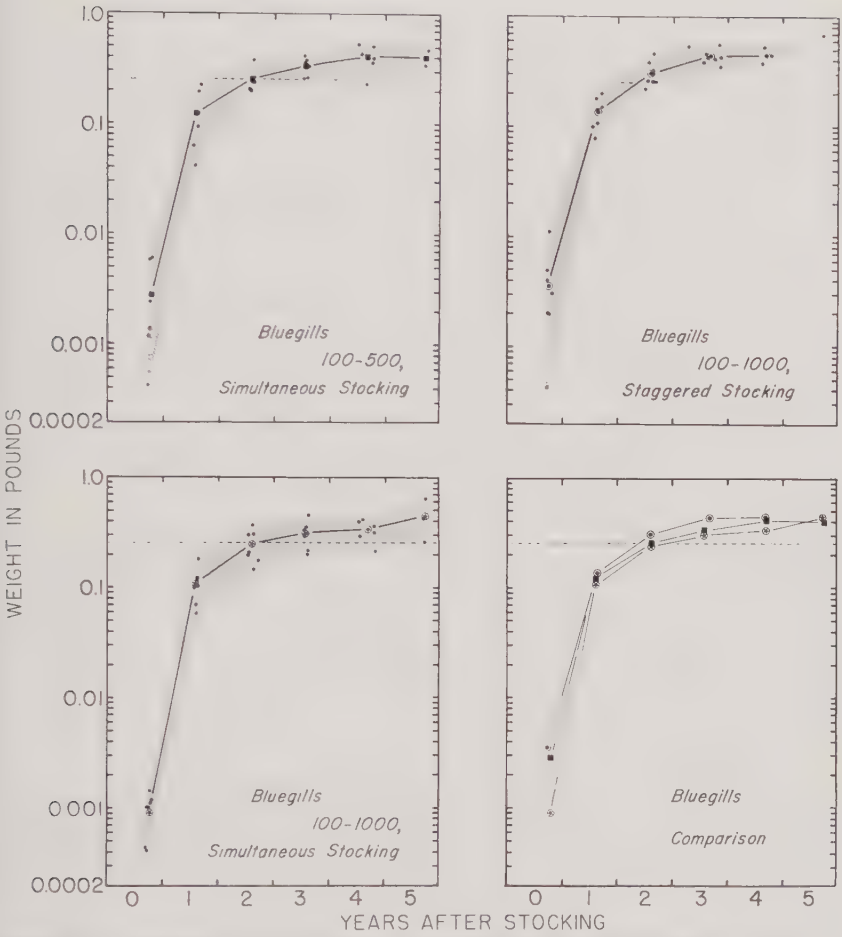


Figure 10. Summary and comparison of growth for the original bluegill stock in three experimental categories.

Bluegill stock attained larger sizes on the whole in ponds where stocking was staggered than in those where it was simultaneous. Bluegills stocked at 500 per acre were on the average larger than those stocked at 1,000 per acre. Category means for size attained ranked in inverse order compared with means in the percentage of survival (Figures 8 and 10).

Differences between category means were considerable, though not large when within-category variation is taken into account. Since some of the between-category differences may have been due to differences in size at stocking, as well as to pond differences, it cannot be concluded that differences in the mean size attained were due to differences in stocking rates used, though the evidence is suggestive.

Some bluegills in some ponds of all three categories attained harvest-

able size during the first summer following stocking (data not shown). Most bluegills in most ponds of all three categories became harvestable during the second summer. Most bluegills in one pond of each of the simultaneous categories failed to reach harvestable size until 4 years after stocking.

The largest two bluegills captured were 8.8 inches and 0.74 pound, and 9.0 inches and 0.67 pound; these were taken during their sixth growing season (age V+).

Relation of Growth to Density of Original Stock In the three bass-bluegill categories, stocking rates were supposed to have been 500 or 1,000 per acre for bluegills and 100 per acre for bass. But on the basis of revised estimates of pond area (see section on stocking data), the actual stocking rates were different in most cases. Most of the errors were less than ±10 per cent; maximum errors were −30 and +50 per cent. Data presented here are actual densities, i.e., number per acre on the basis of revised estimates of mean pond area.

Data on growth of bluegills (Figure 10) contain evidence that the growth of original stock was more rapid at lower densities than at higher densities. The hypothesis that growth was not affected by density for

Table 5. Summary of Computations to Determine If Growth Rates of Original Stock Were Density Dependent *

Age of population	Regression estimates §		Test of significance of b-($\beta = 0$)		
	a	b †	t-value	Degrees of freedom	Probability level ‡
Bass					
I+.....	0.250	+6.50	1.65	19	0.12
II+.....	0.668	−6.32	0.13	18	>0.5
III+.....	1.133	−41.20	0.43	18	>0.5
IV+.....	1.556	−100.90	0.50	16	>0.5
V+.....	1.535	+8.59	0.03	7	>0.5
Bluegills					
I+.....	0.148	−0.56	0.28	18	>0.5
II+.....	0.321	−1.90	0.46	18	>0.5
III+.....	0.428	−4.18	0.60	17	>0.5
IV+.....	0.425	−3.92	0.53	13	>0.5

* Statistics given for regression of mean weight on number of survivors for successive years after stocking.

§ Symbols as defined in Steel and Torrie (1960); e.g., the regression equation of mean weight (Y) on number of survivors (X) for I+ largemouth bass is $Y = 0.250 + 6.50 \times 10^{-4} X$.

† Multiply all tabulated values of b by 10^{-4}.

‡ All were non-significant.

the original bluegill stock was tested, but first, a similar test was made for bass.

To test the hypothesis that growth of the original bass stock was density dependent, simple linear regression equations were computed in which the independent variable was the number stocked per acre and the dependent variable was the mean weight; both statistics were derived from inventory data. Data for individual ponds from all three experimental categories were lumped for each species for each year after stocking. Regression estimates are summarized in Table 5.

If the hypothesis that size attained was unrelated to density of survivors is true, then the slopes of the regression lines should not differ significantly from zero. The *t*-test was used to test the significance of the differences between the estimated slope and zero. The *t* values, and probability of getting a larger value by chance when no difference existed, are tabulated for each regression estimate in Table 5. Differences were all found to be non-significant.

All estimated slopes were negative in the four bluegill regressions. If the null hypothesis were correct, then the probability of getting negative slopes in all four regression estimates by chance is $(\frac{1}{2})^4 = \frac{1}{16} = 0.06$. This probability is small; the author considers this as evidence, though not conclusive, that growth of the original bluegill stock was density dependent to some extent.

There was little evidence that growth of the original bass stock was density dependent over the density range observed. Absolute differences in density were not as large for bass as for bluegills.

GROWTH OF YEAR CLASSES SPAWNED IN THE PONDS It has often been observed that when a new species is introduced into a suitable environment, the growth rate of the original stock is more rapid than that of succeeding year classes. This was also found to be the case with bass and bluegills in project ponds. In the following discussion, "selected year class" denotes a year class hatched in the pond that could be identified reliably over the years involved.

Table 6 shows the estimated mean weights attained by selected year classes at the end of successive growing seasons, except the first season. All but one of the selected year classes were the first spawned in the pond; the one exception (bluegills in the Foster pond) was the second year class and followed a very small first year class. The examples used are based on quite reliable data and seem typical of the various sizes of first year classes spawned in the ponds.

Mean weights for bass year classes were estimated by interpolating between estimates of mean weight derived from successive midsummer or autumn inventories. Mean weights of bluegill year classes at the end of successive growing seasons were estimated by back-calculation using scales (Regier, 1962b).

Table 6. Growth of Selected Year Classes of Bass and Bluegills Spawned in Certain Farm Ponds

Pond	Relative size of year class	Mean weight at end of growing season		
		Second	Third	Fourth
Bass				
Foster	large	0.03	0.13	0.16
Arnot K-2	moderate	0.13	0.19	0.26 *
Lange	moderate	0.11	0.25	..
Arnot K-3	small	0.20	0.48 *	0.58 *
Bluegills				
Arnot K-5	large	0.02	0.07	0.11
Agronomy A	large	0.04	0.08	0.16 *
Hatchery H	moderate	0.06	0.16 *	0.37 §
Foster	small	0.04	0.17 *	..

* Some members of year class had attained harvestable size.
§ Most or all members had attained harvestable size.

Data in Table 6 contain evidence that growth rates of these year classes of both bass and bluegills were density dependent. Thus the larger year classes grew less rapidly than the smaller year classes; the ranges in density of these year classes (data not shown) were considerably greater than was the case with original stock. Also the fish of succeeding year classes were soon in competition with the original stock or subsequent year classes. It may be for the above reasons that growth rates seemed to be more pronouncedly density dependent in these year classes than in the original stock.

Growth of the first year classes spawned in the ponds was considerably slower than that of the original stock. Most bass of the original stock attained harvestable size (10 inches, 0.55 pound) at age II+; most bass in small first year classes did not attain this size until III+, and larger year classes usually not until IV+ or V+. Original bass stock usually spawned first at age II+. An obvious implication for management is that the original bass stock must usually bear the brunt of bass fishing for the first 5 years after stocking. However, if the pond owner is willing to harvest 8- or 9-inch bass, then the first year class spawned in the pond would begin to provide sport about 4 years, or occasionally 3 years, after stocking.

The data show that small bluegill year classes attained harvestable size (6.5 inches, 0.25 pound) at age III+, and larger year classes at about V+; the original stock usually attained harvestable size at II+. Since

bluegill stock frequently spawn during the first summer after stocking, the first year class spawned in the pond begins to provide considerable fishing 4 to 6 years after the original stocking. If the pond owner considers smaller bluegills harvestable (say 5.2 inches, 0.10 pound), then the first year class may provide fishing 3 to 4 years after the original stocking. Thus the original bluegill stock must support all fishing for at least the first three years after stocking, and frequently for the fourth and fifth years as well.

Reproduction

Collection of reproduction data has been discussed briefly in a preceding section; further details are given here. A summary of the data follows, they are then examined for evidence on the following questions. At what age did bass and bluegills first reproduce? Did bluegills stocked as small fingerlings reproduce less successfully at age I+ than did bluegills that were larger when stocked? Did reproductive success differ in the three categories? Within a pond, was success of bluegill reproduction influenced by success of bass reproduction in the same summer? Was reproductive success of bass and bluegills influenced by crowded bluegill populations? Finally, did mean seasonal water temperature affect bluegill reproductive success?

Method of Estimating Reproductive Success Data on reproduction came from the following sources: midsummer inventories, 1954–1957; autumn inventories, 1958; autumn reproduction checks, 1957–1958; late summer reproduction checks, 1958–1960.

Reproductive success was estimated from the observed relative abundance of young-of-the-year fish. In the 1954–1957 period, some pond inventories were made before reproduction had occurred; in such cases relative reproductive success was inferred from the next year's inventory data or from an autumn reproduction check in 1957. It is clear that estimates of reproductive success depend not only on spawning and hatching success, but also on survival to the time of sampling.

Four classes were used to define relative reproductive success of a particular species. Class O denotes cases where no evidence of reproduction was found, though in some cases relatively unsuccessful reproduction probably had occurred. Class 1, or light reproduction, includes those cases where intensive seining[6] resulted in the capture of only several bass of age 0+ and a few dozen or less 0+ bluegills. Under Class 2, or moderate reproduction, several 0+ bass and a dozen or two 0+ bluegills could be captured in most well executed hauls with a 10-foot seine. Class 3, or heavy reproduction, was indicated when about 10 or more

[6] Seining for young fish was considered intensive when about 10 careful hauls were made with a 10-foot minnow seine, or one haul with a 75-foot small-mesh seine, or both.

TABLE 7. SUMMARY OF DATA ON REPRODUCTIVE SUCCESS OF BASS AND BLUEGILLS IN POND POPULATIONS OF THREE EXPERIMENTAL CATEGORIES

Pond	Year stocked	Years after stocking *						
		1	2	3	4	5	6	7
100-500 simultaneous								
Arnot K-3	1953	0–2	1–3	1–1	2–2	1–1	1–3	0–2
Barrett CC	1954	0–1	0–3	2–1	3–2	0–2	0–2	..
Cotton-Hanlon	1954	0–2	3–3	1–1	1–1	2–2	1–2	..
Fell-Moser	1953	0–0	1–3	0–2	2–0	..	..	..
A. Hayes	1953	0–3	1–3	1–2	2–3	0–2	0–2	1–2
Moore	1954	0–3	3–3	0–2	3–1	2–1	0–2	..
Mean		0–1.8	1.5–3.0	0.8–1.5	2.2–1.5	1.0–1.6	0.4–2.2	0.5–2.0
100-1,000 simultaneous								
Arnot K-2	1953	0–1	1–3	1–1	1–1	1–1	1–2	0–3
Arnot K-5	1953	0–0	0–3	1–2	1–1	0–1	..	..
Barrett Rw	1954	0–3	2–1	1–1	2–2	2–2	1–2	..
Catherwood	1954	0–3	0–3	2–3	1–3	1–3	0–3	..
Lange	1954	0–1	1–3	1–1	1–2	0–3	2–1	..
Warren I	1953	0–3	3–3	0–1	§–2	§–1	1–2	2–2
Warren II	1953	0–1	0–3	0–3	0–1	3–1	2–1	3–2
Mean		0–1.7	1.0–2.7	0.8–1.7	1.0†–1.7	1.1†–1.7	1.2–1.8	1.7–2.3

		100–1,000 staggered						
Agronomy A	1953–1954	0–§	0–3	3–1	1–1	1–2	0–1	..
Alfred II	1954–1955	0–§	3–3	0–2	0–3	..	..	..
Baldwin	1953–1954	0–§	3–1	3–2	1–1	1–1	2–2	1–1
Beattie	1954–1955	0–§	0–1	2–0	0 0	0–2	3 2	..
Foster	1953–1954	0–§	3–1	3–1	1–3	1–3	0–2	1–2
Hatchery H ‡	1952–1953	0–§	3–0	0–1	0–1	0–1	0–2	2–2
Hoffman	1954–1955	0–§	3–0	1–1	1–2	1–2	2–2	..
Lakemont	1954–1955	0–§	3–1	0–1	0–3	2–1	..	..
Mean		0–§	2.2–1.2	1.5–1.1	0.5–1.8	0.9–1.7	1.2–1.8	1.3–1.7

* Numbers under each year correspond to classes of reproductive success described in text; and for each pond the first figure represents bass, the second bluegills.
§ No adult fish present.
† Does not include data for Warren I.
‡ The eighth year's data for this pond were 2–2.

0+ bass and about 50 or more 0+ bluegills were captured in most hauls with a 10-foot seine. The limits between classes are admittedly fuzzy, but the reproduction data are not comprehensive enough to permit perfectly objective distinctions.

Summary of Reproduction Data Table 7 contains a summary of reproduction data for bass and bluegill stock in the three categories.

Bass failed to reproduce at age I+ in all populations of these categories. Bass first reproduced successfully at age II+ in 15 of 21 populations. All bass populations had reproduced at least once at age III+, except in one pond where the bass did not reproduce until V+.

Bluegills reproduced at age I+ in 17 of 21 ponds; all bluegill populations had reproduced at least once at II+. Thus bluegills usually first reproduced successfully a year before bass in ponds of the simultaneous categories. In the eight staggered populations, both species first reproduced in the same year in four ponds, bass reproduced before bluegills in two, and bluegills before bass in the remaining two ponds.

Relation of Bluegill Reproduction to Size at Stocking Stocking data, including size of fish at stocking, were presented in Figure 2. Recapitulating briefly, each year bluegills were sorted by size into different lots which were then stocked, in September or October, in project ponds. Bass were not sorted and bass size was not very different in different years.

Table 8 contains data on the first occurrence of bluegill reproduction, and the relative success of first spawning, for ponds grouped according to the size of bluegills stocked. No significant differences are apparent. The author concludes that bluegills stocked (in autumn in the project area) at 1 inch in total length were as likely to reproduce at age I+ as were bluegills stocked at 2 to 3 inches in total length.

Reproductive Success in the Three Bass-Bluegill Categories When the experiments described in this study were being planned, it was known (Saila, 1950) that bluegills tended to reproduce a year before bass when both species were stocked simultaneously in ponds in central New York. It was also known that bluegills tended to become crowded in such ponds. Project personnel postulated that overabundance of bluegills may have been due largely to their earlier reproduction, and that consequently stocking bass a year before bluegills might lead to more satisfactory results.

On the other hand, the relatively slow growth rates of bass may have been due to bluegill competition. If bluegill stocking rates were reduced perhaps the bass would grow more rapidly and reproduce at age I+, or at least would reproduce more successfully at II+.

The data in Figure 11 present available evidence on reproduction on which the above hypotheses may be judged. Each bar on the graph denotes a category mean of the numerals denoting reproductive success

TABLE 8. RELATIONSHIP BETWEEN SIZE OF BLUEGILLS AT STOCKING AND AGE AT WHICH THEY FIRST REPRODUCED

Length at stocking (inches)	Pond	Age at first spawning	Relative success at first spawning
0.8 to 1.0	Catherwood	I+	3
	Barrett CC	I+	1
	Barrett Rw	I+	3
	Baldwin	I+	1
1.0 to 1.4	Arnot K-2	I+	1
	Arnot K-3	I+	2
	Arnot K-5	II+	3
	Warren I	I+	3
	Warren II	I+	1
	Cotton-Hanlon	I+	2
	Lange	I+	1
1.5 to 1.9	Moore	II+	3
	Alfred II	I+	3
	Lakemont	I+	1
	Foster	I+	1
	Hatchery H	II+	1
1.8 to 2.7	Agronomy A	I+	3
	Beattie	I+	1
	Fell-Moser	II+	3
	A. Hayes	II+	3
	Hoffman	II+	1

(of bass or bluegills) in the designated year following stocking. Differences between the two simultaneous categories were minor with respect to bluegills. However, bass reproductive success averaged considerably higher for the 100-500 populations in Year 4 than for the 100-1,000 population, and considerably lower in Years 6 and 7. There were few replicates per category in Year 7. The author can suggest no explanation for the observed differences between simultaneous ponds other than "chance occurrence".

There is evidence in Figure 11 that bass reproduction may have been significantly more successful and bluegill reproduction less successful, during the first two years after stocking of each species, in staggered populations than in the simultaneous ones. Except for those periods there was little difference, at least between the 100-1,000 simultaneous and 100-1,000 staggered categories.

Two hypotheses were tested (data not shown) on the basis of exact probabilities in 2 x 2 tables (Steel and Torrie, 1960; Mainland, 1948). The first was that bass reproduced equally successfully in both simultaneous and staggered categories for two years after they were stocked. The second was that bluegills reproduced equally successfully in both

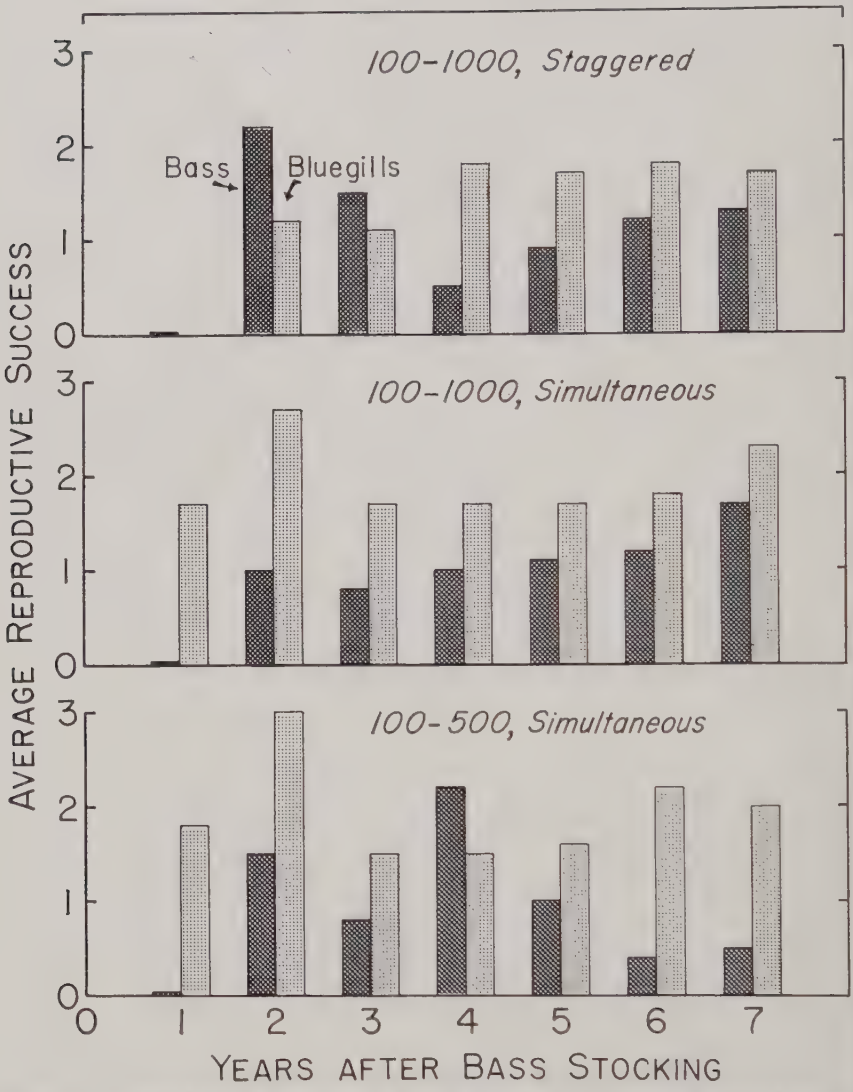


Figure 11. Comparative reproductive success of bass and bluegills in three experimental categories.

categories for two years after being stocked. Results indicated rejection of the second hypothesis, but not the first.

Data in Table 7 suggest that reproductive success may have been more variable in the ponds where stocking was staggered than in those where it was simultaneous. The hypothesis of no difference in this respect was tested using the chi-square test of independence, i.e., to determine if observations on staggered categories contained significantly higher proportions of Class 0 and Class 3 fish than did observations on

the simultaneous categories. Differences were found to be non-significant (Regier, 1961).

Effect of Bass Reproduction on Bluegill Reproduction during the Same Year In project ponds, bass usually spawned between mid-May and mid-June; bluegill spawning was probably restricted to the period between mid-June and mid-August. Is there evidence that 0+ bass preyed to a significant extent on 0+ bluegills?

Table 9 contains a summary of bluegill reproduction data grouped according to the level of bass reproductive success. If 0+ bass preyed extensively on 0+ bluegills, then the reproductive success of bluegills

Table 9. Data on Average Reproductive Success of Bluegills in Three Experimental Categories, Summarized to Permit a Test of Hypothesis That Level of Reproductive Success for Bass Influenced That for Bluegills Later in the Same Year

Experimental category	Reproductive success for bass *			
	0	1	2	3
100-500 simultaneous	2.1 (9)	2.0 (11)	1.5 (6)	2.2 (4)
100-1,000 simultaneous	2.4 (11)	1.9 (14)	1.7 (7)	2.0 (3)
100-1,000 staggered	1.5 (15)	1.8 (10)	1.5 (6)	1.2 (10)
Mean	1.9 (35)	1.9 (35)	1.6 (19)	1.6 (17)

* Data for all years following bass stocking. Figures in parentheses represent number of ponds involved in each case.

in ponds containing abundant 0+ bass should have been lower than that in ponds with few or no 0+ bass. The differences noted in Table 9 are clearly non-significant. The author infers that predation by 0+ bass on 0+ bluegills was usually not pronounced enough to affect bluegill reproduction seriously.

Effect of Crowded Bluegill Populations on Bass and Bluegill Reproduction Swingle (1947) stated that crowded bluegill populations feed on their own young occasionally and will eat their own eggs as well as those of other species of fish. If hungry bluegills in crowded populations frequently behave in this manner, then bass and especially bluegill reproductive success should be lower in ponds where the bluegill population is crowded than in ponds where it is not.

Table 10 shows the average reproductive success of bass and bluegills in project ponds with relatively large and relatively small bluegill

Table 10. Comparison of Average Reproductive Success for Bass and Bluegills in Populations Having Large Standing Crops of Bluegills with That in Populations Having Smaller Standing Crops of Bluegills *

Size of bluegill population	Average reproductive success		Number of populations
	Bass	Bluegills	
Relatively large §.....	1.31	1.56	16
Relatively small †.....	0.92	1.53	36

* Data for first two years following bass stocking not included.
§ Total standing crops of bluegills ranged from 202 pounds per acre in a moderately fertile pond to 526 in a highly fertile pond.
† Total standing crop of bluegills was less than 200 pounds per acre in each case.

populations. Average reproductive success of bluegills was slightly higher where bluegill populations were large than where they were low; average reproductive success of bass differed little in the two groups. The author concludes that density of the bluegill population did not markedly affect the reproductive success of either bass or bluegills.

Effect of Water Temperature on Bluegill Reproduction It is generally held that bluegills require a temperature of 80° F. or more to spawn (Rounsefell and Everhart, 1953), while largemouth bass require temperatures of over 60° F. according to Kramer and Smith (1960). Saila (1950) showed that surface water temperature in one of the project ponds exceeded 80° F. for a period of about 5 weeks in 1949. Maximum surface temperature during this period was 83° F., and only one burst of spawning occurred. After the temperature dropped below 80° F., Saila found ripe male and female bluegills and felt that low temperatures prevented a second period of spawning. Since the surface temperature in this pond did not rise much above the minimum required for bluegill spawning, it might be that bluegill reproduction in this and other project ponds was limited in cool summers by low water temperatures.

The foregoing postulate cannot be tested directly with project data since pond water temperatures were measured infrequently. However, data on total solar radiation are available for the years in which the experiments were made. The author considers it likely that maximum midsummer temperatures were positively correlated with total solar radiation during the summer.

Data in Table 11 show that the estimated average reproductive success of bluegills was highest in 1960 when total solar radiation during June, July and August was lowest. Also, bluegill reproductive success was lowest in 1957, one of the two years when radiation was highest. The author concludes that bluegill reproductive success was not seriously limited by relatively lower water temperatures found in project ponds during cool summers.

Table 11. Comparison of Average Reproductive Success for Bluegills with Approximate Total Solar Radiation During June, July and August*

Item	1956	1957	1958	1959	1960
Total solar radiation §	46	50	47	50	38
Average reproductive success for bluegills	1.55 (11)	1.38 (21)	1.70 (20)	1.95 (18)	2.00 (16)
Average reproductive success for bass†	1.30 (10)	1.05 (20)	1.11 (18)	1.12 (17)	1.19 (16)

* Data from first two summers after stocking of bass not included. Figures in parentheses represent number of ponds involved in each case.

§ Total solar radiation, in kgm cal/cm², for June, July and August of respective years. Radiation measured on horizontal surface on top of Plant Science Building, Cornell University. Data from summary by Division of Meteorology, Department of Agronomy, Cornell University.

† Largemouth bass generally spawn when water temperatures are 65° to 70° F. Thus bass reproductive success was likely not affected by maximum summer temperatures or total solar radiation. Bass data are included to indicate similarity over the years.

Standing Crops

Standing crops were estimated for each size stratum (large or harvestable, intermediate, small) of each species. Precision of standing crop estimates is examined briefly. Data on standing crops during successive years after stocking are then summarized, and differences between experimental categories and between ponds of different fertilities within categories are explored. Finally, standing crops of original stock are estimated for hypothetical cases where no harvesting occurs.

Precision of Standing Crop Estimates Standing crops of harvestable and intermediate size strata were estimated by the product of the estimated population number and the estimated mean weight. Standing crops of small size strata were estimated as follows: Total or almost total populations of small bluegills and small bass were captured in eight partially drained ponds in 1958. Data on relative abundance of small bass and bluegills were collected at all other inventories over the years of the project. By relating the relative abundance of small fish where their standing crops were unknown to that where the standing crops were known, a *rough* estimate of standing crops of small bass and bluegills could be made for each year in each pond.

An example may clarify the method. Pond A was seined and small bluegills, in this case less than 2 inches long, were found to be abundant. When Pond A was drained the standing crop was found to be 30 pounds per acre. Pond B was seined and small bluegills, also less than 2 inches long, were found to be only about half as abundant as in Pond A. The

standing crop in Pond B was estimated to be $30 \times \frac{1}{2} = 15$ pounds per acre.

Standing crops are given in pounds per acre of pond surface area. The figure used for pond area is the estimated mean pond size during the growing season.

Estimates of standing crops, in the intermediate and large size strata, are thus the products of three estimates: a Petersen estimate of population size, an estimate of mean weight based on a more-or-less-random sample, and the inverse of an estimate of pond size. Each of the three is, of course, subject to error, as is the method of estimating standing crops in the small size strata. Part of the variability in standing crop data is to be ascribed to errors in estimates. Errors might be quite large, e.g., if it happened that pond size were under-estimated by 10 per cent, but both population size and mean weight were overestimated by 10 per cent, the standing crop would be overestimated by about 33 per cent.

Summary of Data on Standing Crops Tables 12, 13 and 14 contain summaries of standing crops at time of inventory for largemouth bass, bluegills, and bass plus bluegills, respectively, in the three experimental categories. All estimates are given in units of pounds per acre. Time of inventory was usually midsummer, except that an autumn inventory was used for the last year's estimate in each population. Two summaries of the bass data are given in Table 12; one shows total standing crops and the other shows standing crops of harvestable bass. Similar summaries are given for bluegills in Table 13. A single summary is given for bass plus bluegill data in Table 14 showing the over-all total standing crops.

Estimated harvests that were made between consecutive inventories are also given. Since few subharvestable bass were removed the estimates in the first part of Table 12 are identical in most cases with those in the second part. Harvest data were seldom sufficiently detailed to permit estimates of harvests of bluegills over 6.5 inches long; Table 13, therefore, contains only total harvest estimates. Harvests are discussed further in a subsequent section.

Certain data were omitted from consideration in this section. Some of these were from ponds (Barrett Rw and Lakemont) that leaked badly and were subject to marked water level fluctuations. Barrett Rw was also contaminated with brown bullheads in the latter years. The last two years' data from the Warren I pond were deleted because of a severe summerkill, and the last year's data from the Fell-Moser pond because of a severe winterkill. The tabulated data, therefore, apply to bass-bluegill populations that had not suffered severe kills, that occurred in ponds not subject to marked water level fluctuations and that were not contaminated, or contaminated only to a negligible extent, by other fish species.

In each table, the populations within experimental categories are grouped according to estimated pond fertility. Effects of pond fertility levels on standing crops are explored in the next section.

It is apparent from Tables 12 to 14 that the size of bass-bluegill populations (measured by total standing crop) frequently did not increase regularly until the carrying capacity was attained; rather increases were often delayed for a number of years and then might be explosive. Such explosions occurred more frequently with bluegills than with bass; the large numbers of subharvestable bluegills then became the major component, by weight, in the fish population.

Perhaps the most striking observation is the great variability both within the same pond over a number of years and among ponds within categories, even among ponds within fertility levels within categories. However, the variability is not unexpected in view of the findings under previous sections. Thus survival and growth rates of original stock varied considerably, and growth rates did not seem to be markedly influenced by the density of survivors, i.e., growth and survival rates seemed to vary independently. First reproduction did not always occur the same number of years after stocking, and the size of year classes varied greatly. Furthermore, rates of harvest were not constant. Since standing crops depended on each of these factors, and others, it is not surprising that the variability in standing crops was marked. The author found it impossible to explain observed differences in each of the factors mentioned, and will not attempt to explain individual differences in standing crops. However, some differences between groups of populations may be examined briefly.

Relation of Standing Crops to Relative Pond Fertility

Direct measurements of pond fertility were not attempted in this study; however, project personnel obtained and maintained records of fertilizer added directly to each pond. All ponds of the three bass-bluegill categories were either built on agricultural lands (from which they presumably received fair amounts of nutrients in runoff), or were fertilized directly, or both. Thus all ponds were either very fertile or fairly fertile; none was clearly infertile.

Ponds were divided into two classes, those judged to be of relatively high fertility and those of moderately high fertility. Ponds that had received fairly large amounts of fertilizer regularly, or had received limited runoff from highly fertile watersheds, or both, were considered highly fertile. All the rest were considered moderately fertile.

Tables 12, 13 and 14 contain standing crop data summarized by ponds within fertility levels in the several experimental categories. The means of total standing crops (and harvests) for bass and bluegills are summarized by fertility levels within categories in Table 15. Within categories, the mean standing crops were generally higher in the highly

Table 12. Estimated Standing Crops and Harvests of Bass in Ponds of Three Experimental Categories Annually after Stocking *

Experimental category	Relative pond fertility	Pond §	Quantity stocked	Year 1		Year 2		Year 3		Year 4		Year 5 crop
				Crop	Harvest	Crop	Harvest	Crop	Harvest	Crop	Harvest	
			Total standing crops and harvests									
100-500 simultaneous	High	Arnot K-3	1	27	0	28	10	27	0	25	0	30
		Moore	1	51	0	77	0	87	35	67	..	..
		Fell-Moser	1	36	0	40	10	42	0	70	..	..
	Moderate	Barrett CC	1	20	15	20	15	12	0	17	..	..
		Cotton-Hanlon	1	13	10	20	10	18	0	18	..	..
		A. Hayes	1	38	0	40	0	49	10	48	..	..
100-1,000 simultaneous	High	Arnot K-2	1	18	0	35	10	69	0	70	0	60
		Arnot K-5	1	25	0	33	0	29	0	31	0	30
		Warren I	1	12	0	36	10	58	..	..	..	..
		Warren II	1	25	0	45	5	58	0	59	0	100
	Moderate	Catherwood	1	13	0	24	5	28	5	40	..	..
		Lange	1	24	25	36	25	73	10	62	..	..
100-1,000 staggered	High	Agronomy A	1	15	0	63	0	38	0	65	20	52
		Beattie	1	41	15	42	10	54	0	73	20	49
		Hatchery H	1	64	0	99	15	55	15	73	30	56
		Hoffman	1	20	10	41	10	28	10	33	..	..
	Moderate	Alfred II	1	17	10	33	5	38	10	6	..	..
		Baldwin	1	21	0	60	5	90	0	107	0	168
		Foster	1	16	0	38	20	46	0	108	45†	66

Standing crops and harvests of bass over 10.0 inches long

100-500 simultaneous	High	Arnot K-3	..	0	0	0	10	20	0	13	0	26
		Moore	..	2	0	47	0	76	35	60	..	..
		Fell-Moser	..	2	0	37	10	40	0	67	..	..
	Moderate	Barrett CC	..	0	0	0	15	10	0	3	..	..
		Cotton-Hanlon	..	0	10	19	10	15	0	12	..	..
		A. Hayes	..	0	0	39	0	44	10	41	..	..
100-1,000 simultaneous	High	Arnot K-2	..	0	0	32	10	34	0	22	0	20
		Arnot K-5	..	0	0	21	0	28	0	20	0	18
		Warren I	..	0	0	22	10	24	..	..	..	..
		Warren II	..	0	0	45	5	58	0	59	0	68
	Moderate	Catherwood	..	0	0	0	5	4	5	35	..	..
		Lange	..	0	25	33	25	39	10	25	..	..
100-1,000 staggered	High	Agronomy A	..	0	0	63	0	34	0	42	20	25
		Beattie	..	0	15	42	10	50	0	60	20	8
		Hatchery H	..	30	0	95	15	44	15	32	30	16
		Hoffman	..	0	10	33	10	14	10	4	..	..
	Moderate	Alfred II	..	0	10	29	5	12	10	6	..	..
		Baldwin	..	0	0	53	10†	78	0	65	0	93
		Foster	..	0	0	35	20	33	0	31	45†	2

* Data in pounds per acre.
§ Ponds within categories grouped according to author's judgment of their relative fertility.
† Part of harvest taken by seining.

Table 13. Estimated Standing Crops and Harvests of Bluegills in Ponds of Three Experimental Categories Annually after Stocking *

Experimental category	Relative pond fertility	Pond §	Quantity stocked	Year 1		Year 2		Year 3		Year 4		Year 5 crop
				Crop	Harvest	Crop	Harvest	Crop	Harvest	Crop	Harvest	
			Total standing crops and harvests									
100-500 simultaneous	High	Arnot K-3	1	45	0	67	40	92	25	218	5‡	160
		Moore	1	82	15	125	75	168	70	245	..	..
		Fell-Moser	3	77	0	140	55	261	300‡	213	..	..
	Moderate	Barrett CC	1	12	20	72	20	106	15‡	138	..	..
		Cotton-Hanlon	1	19	10	20	10	79	25	186	..	..
		A. Hayes	3	80	35‡	40	0	69	5	86	40	329
100-1,000 simultaneous	High	Arnot K-2	1	130	0	169	100‡	78	25‡	154	10‡	325
		Arnot K-5	1	44	0	66	0	109	5	309	50‡	311
		Warren I	1	17	40‡	58	50	69	..	..	..	..
		Warren II	1	81	0	160	125†	48	2	127	60†	309
	Moderate	Catherwood	1	51	0	92	5	202	18†	229	..	..
		Lange	1	73	40	86	20	151	40	344	..	..
100-1,000 staggered	High	Agronomy A	11	55	0	468	195	526	190	511	..	..
		Beattie	5	23	5	44	0	51	5	13	..	..
		Hatchery H	3	53	0	64	3	95	25	48	0	109
		Hoffman	4	20	15	40	20	88	..	..	..	..
	Moderate	Alfred II	2	86	0	364	65†	152	..	..	..	..
		Baldwin	1	29	0	38	0	56	0	55	..	..
		Foster	2	13	5	33	0	100	20‡	96	..	..

Standing crops of bluegills over 6.5 inches long, i.e., harvestable

100-500 simultaneous	High	Arnot K-3	..	0	..	0	..	26	..	25	..	52
		Moore	..	0	..	66	..	60	..	7	..	..
		Fell-Moser	..	0	..	95	..	39	..	12	..	..
	Moderate	Barrett CC	..	0	..	31	..	74	..	24	..	..
		Cotton-Hanlon	..	0	..	11	..	16	..	20	..	..
		A. Hayes	..	0	..	19	..	49	..	57	..	..
100-1,000 simultaneous	High	Arnot K-2	..	0	..	54	..	41	..	43	..	139
		Arnot K-5	..	0	..	10	..	76	..	59	..	29
		Warren I	..	0	..	47	..	13	..	..	..	..
		Warren II	..	0	..	151	..	10	..	6	..	33
	Moderate	Catherwood	..	0	..	0	..	109	..	145	..	..
		Lange	..	0	..	0	..	0	..	100	..	..
100-1,000 staggered	High	Agronomy A	..	0	..	69	..	28	..	120	..	..
		Beattie	..	0	..	36	..	47	..	1	..	..
		Hatchery H	..	0	..	62	..	43	..	4	..	107
		Hoffman	..	0	..	27	..	3	..	..	..	..
	Moderate	Alfred II	..	0	..	70	..	56	..	..	..	..
		Baldwin	..	0	..	6	..	44	..	44	..	..
		Foster	..	0	..	32	..	86	..	46	..	..

* Data in pounds per acre.
§ Ponds within categories grouped according to author's judgment of their relative fertility.
† Part of harvest taken by seining.
‡ All of harvest taken by seining.

TABLE 14. ESTIMATED TOTAL STANDING CROPS AND HARVESTS OF BASS AND BLUEGILLS IN PONDS OF THREE EXPERIMENTAL CATEGORIES ANNUALLY AFTER STOCKING BASS *

Experimental category	Relative pond fertility	Pond §	Quantity stocked	Year 1		Year 2		Year 3		Year 4		Year 5 crop
				Crop	Harvest	Crop	Harvest	Crop	Harvest	Crop	Harvest	
100-500 simultaneous	High	Arnot K-3	2	73	0	95	50	119	25	243	5	190
		Moore	1	133	15	202	75	255	105	312	..	..
		Fell-Moser	4	113	0	180	65	303	300	283	..	..
	Moderate	Barrett CC	1	32	35	92	35	118	15	155	..	..
		Cotton-Hanlon	1	32	20	40	20	97	25	204	..	..
		A. Hayes	4	118	35	80	0	118	15	134	..	..
100-1,000 simultaneous	High	Arnot K-2	2	148	0	204	110	147	25	224	10	385
		Arnot K-5	2	69	0	99	0	138	5	340	50	341
		Warren I	2	29	40	94	60	127	..	..	..	..
		Warren II	2	106	0	205	130	106	2	186	60	409
	Moderate	Catherwood	1	64	0	116	10	230	23	269	..	..
		Lange	1	97	65	122	45	224	50	406	..	..
100-1,000 staggered	High	Agronomy A	1	26	0	118	0	506	195	591	210	563
		Beattie	1	46	15	65	15	98	0	124	25	62
		Hatchery H	1	67	0	152	15	119	18	168	55	104
		Hoffman	1	24	10	61	25	68	30	121	..	..
	Moderate	Alfred II	1	19	10	119	5	402	75	158	..	..
		Baldwin	1	22	0	89	5	118	0	163	1	223
		Foster	1	18	0	51	25	79	0	208	65	172

* Data in pounds per acre.
§ Ponds within categories grouped according to author's judgment of their relative fertility.

fertile pond groups than in the moderately fertile ones; however, the differences were not pronounced. No objective test of the significance of observed differences was attempted because the author could devise no way of taking harvests into account. The author considers the evidence as suggestive that the more fertile ponds could support higher standing crops of bass and bluegills than the less fertile ones.

Standing Crops in Three Bass-Bluegill Categories With respect to a particular species in a pond, standing crops during years after stocking clearly depend on numbers stocked, survival and growth rates of original stock, success of reproduction, and survival and growth of year classes born in the pond.

From data on survival of the original bass stock, the author concluded that no significant differences existed between coefficients of natural mortality in the three experimental categories. Growth rates of the original bass were considered not significantly different in the three categories and growth did not seem density dependent. Bass reproduction seemed to be somewhat more successful, 2 years after stocking, in ponds of the staggered category than in ponds of the simultaneous categories. Mean harvests were approximately equal in the three categories. Judging from these findings, one would expect that means of the total standing crops of bass should have been quite similar in the three categories during the first, second and third years after stocking. Subsequently, total standing crops of bass should have been somewhat higher in the staggered category, due to the generally more successful reproduction in Year 2, than in the simultaneous categories. Data on total standing crops of bass in Table 16 tend to indicate that the above inference held true.

A similar "prediction" may be attempted based on previously analyzed bluegill data. Natural mortality coefficients were approximately equal in the two simultaneous categories, and in the staggered category after the first 15 months when mortality was considerably higher than in subsequent years. Thus after Year 1, survivors of the original bluegill stock were approximately in the proportions of 1.0 : 2.0 : 0.8 in the 100-500 simultaneous, 100-1,000 simultaneous, and 100-1,000 staggered categories, respectively. Growth of this stock may have been somewhat density dependent since the mean sizes attained were approximately in the proportions 1.0 : 0.9 : 1.2, respectively, for the same categories. Reproduction seemed to be more successful during the first two years after stocking in ponds of the simultaneous categories than in ponds of the staggered category. Harvests were roughly equal in the three categories. On this basis, one might predict that the total standing crops of bluegills would have averaged highest in the 100-1,000 simultaneous category, next in the 100-500 simultaneous category, and lowest in the

TABLE 15. MEAN ESTIMATED TOTAL STANDING CROPS AND HARVESTS OF BASS AND BLUEGILLS IN THREE EXPERIMENTAL CATEGORIES, ACCORDING TO POND FERTILITY, ANNUALLY AFTER STOCKING *

Experimental category	Relative pond fertility	Quantity stocked	Year 1		Year 2		Year 3		Year 4		Year 5 crop
			Crop	Harvest	Crop	Harvest	Crop	Harvest	Crop	Harvest	
Bass §											
100-500 simultaneous	High	1	38	0	48	7	52	12	54	0	30
		(3)	(3)		(3)		(3)		(3)		(1)
	Moderate	1	24	15	27	8	26	3	28	0	33
		(3)	(3)		(3)		(3)		(3)		(1)
100–1,000 simultaneous	High	1	20	0	37	6	54	0	53	0	63
		(4)	(4)		(4)		(4)		(3)		(3)
	Moderate	1	18	12	30	15	50	8	51	..	..
		(2)	(2)		(2)		(2)		(2)		(0)
100-1,000 staggered	High	1	35	6	61	9	44	6	61	23	52
		(4)	(4)		(4)		(4)		(4)		(3)
	Moderate	1	18	3	44	10	58	3	74	22	117
		(3)	(3)		(3)		(3)		(3)		(2)
All combined	High	1	30	3	49	8	49	6	58	9	54
		(11)	(11)		(11)		(11)		(10)		(7)
	Moderate	1	20	10	35	12	42	3	50	15	89
		(8)	(8)		(8)		(8)		(8)		(3)

Bluegills †											
100-500 simultaneous	High	2 (3)	68 (3)	5	111 (3)	57	174 (3)	132	225 (3)	5	160 (1)
	Moderate	1 (3)	37 (3)	15	44 (3)	10	85 (3)	15	137 (3)	40	329 (1)
100-1,000 simultaneous	High	1 (4)	68 (4)	10	113 (4)	69	76 (4)	11	197 (3)	40	315 (3)
	Moderate	1 (2)	62 (2)	20	89 (2)	12	177 (2)	29	286 (2)	..	..
100-1,000 staggered	High	6 (4)	38 (4)	5	154 (4)	54	190 (4)	73	191 (3)	0	109 (1)
	Moderate	2 (3)	43 (3)	2	145 (3)	22	103 (3)	12	76 (2)	..	..
Bass and Bluegills §											
100-500 simultaneous	High	2 (3)	106 (3)	5	159 (3)	64	226 (3)	143	279 (3)	5	190 (1)
	Moderate	2 (3)	61 (3)	30	71 (3)	18	111 (3)	18	164 (3)	..	..
100-1,000 simultaneous	High	2 (4)	89 (4)	10	150 (4)	75	130 (4)	11	250 (3)	40	383 (3)
	Moderate	1 (2)	80 (2)	32	119 (2)	28	227 (2)	37	338 (2)	..	..
100-1,000 staggered	High	1 (4)	41 (4)	6	99 (4)	18	198 (4)	61	251 (4)	97	243 (3)
	Moderate	1 (3)	20 (3)	3	86 (3)	12	200 (3)	25	176 (3)	33	198 (2)

* Data in pounds per acre; figures in parentheses represent number of ponds involved in each case.
§ Years based on time bass were stocked.
† Years based on time bluegills were stocked.

Table 16. Mean Estimated Total Standing Crops and Harvests of Bass and Bluegills in Three Experimental Categories Annually after Stocking *

Experimental category	Quantity stocked	Year 1		Year 2		Year 3		Year 4		Year 5 crop
		Crop	Harvest	Crop	Harvest	Crop	Harvest	Crop	Harvest	
Bass §										
100-500 simultaneous	1 (6)	31 (6)	7	38 (6)	8	39 (6)	8	41 (6)	0	32 (2)
100-1,000 simultaneous	1 (6)	19 (6)	4	34 (6)	9	52 (6)	3	52 (5)	0	63 (3)
100-1,000 staggered	1 (7)	28 (7)	5	54 (7)	9	50 (7)	5	67 (7)	23	78 (5)
All combined	1 (19)	26 (19)	6	43 (19)	10	46 (19)	5	54 (18)	11	65 (10)
Bluegills †										
100-500 simultaneous	2 (6)	52 (6)	10	78 (6)	34	130 (6)	74	181 (6)	22	244 (2)
100-1,000 simultaneous	1 (6)	66 (6)	13	105 (6)	50	110 (6)	18	233 (5)	40	315 (3)
100-1,000 staggered	4 (7)	40 (7)	4	150 (7)	40	153 (7)	47	145 (5)	0	109 (1)

	Bass and Bluegills §									
100-500 simultaneous	2 (6)	84 (6)	18	115 (6)	41	168 (6)	80	222 (6)	5	190 (2)
100-1,000 simultaneous	2 (6)	105 (6)	17	140 (6)	59	162 (6)	21	285 (5)	40	378 (3)
100-1,000 staggered	2 (7)	32 (7)	5	93 (7)	15	199 (7)	46	219 (5)	71	225 (1)

* Data in pounds per acre; figures in parentheses represent number of ponds involved in each case.
§ Years based on time bass were stocked.
† Years based on time bluegills were stocked.

100-1,000 staggered category. The data in Table 16 bear out this prediction for only the first year following bluegill stocking.

It was postulated that mean standing crops of bluegills should have been lowest in ponds in the staggered category; however, in Year 2 this mean was the highest of the three. The means for these ponds were strongly influenced by the data from the Agronomy A pond. In this highly fertile pond bluegills were stocked as large fingerlings, they reproduced very successfully as yearlings, and the population exploded and attained a total standing crop of 470 pounds per acre during the second summer after stocking. An important point follows from the foregoing discussion: the great variability in standing crop data, and the availability of only a small number of replicates, indicates that the confidence interval about each mean is very broad.

In view of the great variability in total standing crops of bluegills, the author considered observed differences between categories to be nonsignificant. The highest standing crops seemed to result when very successful reproduction, probably largely fortuitous, occurred in very fertile ponds. The result was a crowded population in which the dominant year class might not attain harvestable size until age III+, IV+ or V+.

Table 16 also shows the mean total standing crops of bass plus bluegills in the three categories. Cautions already expressed concerning the interpretation of bluegill data apply to these data as well. The low mean standing crop in Year 1 in ponds of the staggered category was, of course, partly due to the fact that bluegills were stocked a year after the bass. To the extent that the means do estimate what occurred in the "average" pond, the data indicate how standing crops increased during the first four or five years after stocking.

Standing Crops of Unfished Original Stock Data on observed standing crops were summarized in the previous section. Besides the natural variability in survival, growth, and reproduction, there also was variability in harvests. Models of unfished bass and bluegill populations are developed in this section; such models are useful in deriving estimates of possible harvests during the first three to six years of a population's existence.

Table 17 gives hypothetical standing crops of the original bass and bluegills, for successive years following stocking, in "average" ponds of the three categories. These models are based on the following assumptions:

1. Largemouth bass were stocked as fingerlings about September 15; bluegills were stocked as fingerlings about October 1.
2. There was no fishing mortality. Annual natural mortality of bass was 20 per cent in all pond categories, natural mortality of bluegills was 30 per cent per year in all categories, except

during the first 15 months in the staggered category when it was 74 per cent per year. Natural mortality coefficients were constant for the periods indicated. These assumptions are based on means derived from project ponds (see section on survival).

3. Bass and bluegill growth rates were equal to the over-all mean growth rates for each species (i.e., growth rates of original stocks were not density dependent).

The models might, therefore, apply to the "average" unfished population in a moderately fertile pond that had not suffered severe summerkills or winterkills. The bass model indicates that an average standing crop of original bass stock reaches about 50 pounds per acre 3 years after stocking and continues at about this level for several years. The bluegill model for 100-1,000 simultaneous stocking (standard New York bass-bluegill stocking policy) shows a peak of about 140 pounds per acre during the second summer following stocking and decreases after that. The bluegill peak occurs about the time the fish reach harvestable size, 6.5 inches. Standing crops of original bluegill stock in the other two stocking categories are half or less than half those for standard stocking; if growth rates were in fact density dependent the differences would not be so pronounced.

With respect to original stock, it appears that the standard New York stocking policy results in higher standing crops of harvestable bluegills during the first four or five years after stocking than the other two stocking methods tested. After this period there would likely be little difference in production of harvestable bluegills in ponds of the different categories. Average standing crops of harvestable bass probably differ little in ponds of these three categories.

In a subsequent section the author risks the generalization that the above models apply to the average of the better-constructed, better-managed, two-thirds of warm-water farm ponds in New York.

Harvests

Methods by which empirical data on harvests were collected, and the reliability of these data, have been discussed. Harvests in the various individual pond populations have been summarized in Tables 12 to 16 and are discussed further here. Finally, "optimum" rates of harvest of original stock in "average" ponds stocked according to standard policy are estimated, using the models of standing crops given in Table 17.

Method of Estimating Harvests Annual harvests were estimated from records maintained by pond owners and project personnel. In most ponds in the three bass-bluegill categories very little or no unauthorized fishing occurred. However, the following ponds were exceptions at least for the periods indicated: Alfred II, total period; Barrett CC, first two years; Cotton-Hanlon, total period; Lange, last two years. The

Table 17. Models of Standing Crops of Bass and Bluegills in Three Experimental Categories, in the Absence of Fishing, Annually after Stocking

Experimental category	Statistic	Year 0	1	2	3	4	5
Bass							
All three	Number per acre	100	82	66	53	42	34
	Mean weight	0.006	0.29	0.63	0.92	1.22	1.52
	Pounds per acre	1	24	42	49	51	52
Bluegills							
100-500 simultaneous	Number per acre	500	370	260	180	130	90
	Mean weight	0.002	0.12	0.27	0.36	0.39	0.47
	Pounds per acre	1	44	70	65	51	42
100-1,000 simultaneous	Number per acre	1,000	740	520	360	260	180
	Mean weight	0.002	0.12	0.27	0.36	0.39	0.47
	Pounds per acre	2	89	140	130	100	85
100-1,000 staggered	Number per acre	0	1,000	350	210	150	100
	Mean weight	....	0.002	0.12	0.27	0.36	0.39
	Pounds per acre	0	2	42	57	54	39

author made a special effort in 1957 and 1958 to determine the amounts of fish harvested in each of these ponds by interviewing the owners and local persons known to have been at the pond. He then made reasonable estimates of the amounts harvested taking data from interviews and inventories into consideration. Such data are of course less reliable than the more detailed reports submitted by most pond owners.

Harvest estimates were calculated in pounds per acre in terms of the mean surface area during the growing season. Estimates were then rounded to units of 5 pounds because the data did not justify greater precision.

Definitions of Minimum Harvestable Size Minimum harvestable size of bluegills is taken here to be 6.5 inches (about 0.20 to 0.25 pound), for bass it is 10.0 inches (about 0.50 to 0.55 pound). The author believes that these are reasonably accurate estimates of what most project cooperators, and New York State pond owners in general, consider to be the minimum harvestable size. These minima are considerably larger than those that Swingle (1950) found applicable to Alabama ponds, namely, 0.1 pound (about 5.2 inches) for bluegills and 0.4 pound (about 9.0 inches) for bass.

The decision to consider 6.5 inches as the minimum size for bluegills was made in 1960. During the period when the data were being collected, project personnel considered Swingle's lower limit as applicable to New York ponds. Thus cooperators were advised to harvest bluegills over about 5 inches long. Though they did remove some bluegills less than 6.5 inches long from their ponds, many were discarded as too small to eat judging from reports, conversations with cooperators, and actual observation by the author. However, pond owners reported their catches without specifying which were discarded, and their reports were usually not sufficiently detailed to permit estimates to be made of harvests of bluegills over 6.5 inches long. Harvest data are therefore summarized only as total bluegill harvests, and harvests of bluegills over 5.2 inches long.

Summary of Harvest Data Data on harvests made in respective inter-inventory periods in individual ponds are summarized in Tables 12 (bass), 13 (bluegills) and 14 (bass plus bluegills). Estimated mean harvests within ponds of similar fertility within experimental categories are given in Table 15. Finally, Table 16 shows mean harvests within categories for each species, and for both species combined.

The harvests were of two kinds; one involved removing subharvestable fish (usually less than 3.5 inches long) and the other involved harvestable fish. On nine occasions and in eight ponds, project personnel removed part of a crowded year class of subharvestable bluegills in an attempt to alleviate crowding and improve growth. Table 18 contains data on these management efforts. The weight of bluegills removed was not large in most cases; the datum for the Fell-Moser pond seems to be

Table 18. Subharvestable Bluegills Removed in Attempt to Reduce Crowding in Certain Ponds

Pond	Years after stocking bass	Pounds per acre removed	Percentage of year class removed
Alfred II	3	40	20
Arnot K-2	3	25	50
Arnot K-3	3	25	40
Arnot K-5	3, 4	5, 30	5, 15
Barrett CC	3	15	40
Barrett Rw	3	50	50
Fell-Moser	4	260*	80
Warren II	4	40	30

* Probably an overestimate.

an overestimate, judging from subsequent inventory data. About 5 pounds of small bass per acre were removed once from the Baldwin pond for stocking other ponds.

Some harvestable fish were taken by seining and the rest by angling. Harvests made by seining are indicated in Tables 12 to 16; these harvests were made in ponds controlled by Cornell, or were made in private ponds at the owners' requests.

In the autumn of 1955, project personnel removed, by seining, relatively large numbers of the larger bluegills present in three ponds: Arnot K-2, A. Hayes and Warren I. Bluegills removed were all of original stock and of ages II+, I+, and I+, respectively. These fish were removed as part of a test of the hypothesis that growth rates and reproductive success would be greater than average with a relatively large decrease in the standing crop. It seems clear that three replicates were too few for such an experiment, in the light of the discussions in previous sections, of the variability encountered in the various aspects of population dynamics, especially since the populations differed in many respects including the harvest rate. And, in fact, the author was unable to determine any consistent effect of the three experimental harvests on subsequent growth, reproduction and standing crop.

Rates of angling harvest in pounds per acre per year varied greatly between ponds, and between years within ponds. Bass harvests by angling in single inter-inventory periods varied from 0 to 35 pounds per acre (Table 12). Private pond owners caught an average of 10 pounds of bass per acre per year. Bluegill catches varied from 0 to 75 pounds per acre for similar periods, with a mean of about 20 pounds per acre. It seems likely that most of the populations could have supported greater harvests, at least with respect to bluegills.

Only one pond owner made a special effort each year to take both bass and bluegills according to recommendations made by project per-

sonnel. He harvested about 35 pounds per acre of bass and 160 pounds per acre of bluegills during the first four years after stocking. The other pond owners fished their ponds either occasionally or not at all. Because of the marked variability in harvest rates, as in all other population aspects previously considered, the author has not attempted to evaluate the effects of observed harvests on population dynamics.

Optimum Harvest Models for Bass-Bluegill Ponds It was shown in the section on growth rates that most bass in the first year class hatched in a pond first attained harvestable size 6 or more years after the initial stocking. The comparable interval was 4 or more years in the case of bluegills. It follows that the original bass must usually provide all the bass fishing for the first five years after stocking, and bluegills for the first three years. Table 17 contains models of standing crops of unfished original stock. Similar models were constructed in which harvest rates were also taken into account. Optimum harvest rates thus determined are given in Table 19.

Optimum harvest of original stock is here defined as the maximum weight of a particular species that can be harvested between the time when it reaches harvestable size and the time that its progeny reach harvestable size, with the added condition that annual harvests must be equal.

The specific assumptions on which the harvest models were constructed include those (1 to 3) used for the models of standing crops plus the following:

4. Harvests were made in midsummer, about August 1. At first glance this might appear to be an unrealistic assumption; however, the results were very similar to those where harvests were symmetrically distributed, with respect to time, about August 1.
5. The harvests of original stock were unselective with respect to size of individual fish.

Details of estimating the optimum number or weight to be harvested annually require further explanation. Regier (1962a) described a method of estimating the natural mortality coefficient for the case where population size is known for two dates, as well as the numbers harvested on two intermediate dates. Here the procedure is reversed. Now the natural mortality coefficient is known as well as the population size on two dates, and the problem is to estimate the number that may be harvested on specified dates.

Consider the case of largemouth bass in a pond whose owner desires to harvest an equal number of bass each year. He starts with 100 bass (in a 1-acre pond) on September 15 of Year 0, and he wants the last of these original bass to fill his quota on August 1 of Year 5. Assumptions 1 to 5 apply. The problem is to estimate the pond owner's annual quota, starting with 100 bass and ending five years later with 0, and spacing a specified number of equal harvests between.

TABLE 19. SCHEDULES FOR OPTMIUM HARVESTS, FOR AN AVERAGE PROJECT POND, OF ORIGINAL STOCKS OF BASS AND BLUEGILLS STOCKED SIMULTANEOUSLY AT RATES OF 100 AND 1,000 PER ACRE

Species	Harvest quota	Weight or number per acre harvested each year after stocking *						
		1	2	3	4	5	6	Total
Constant number per acre to be harvested each year over specified period								
Bass	11 fish, starting in Year 2	0	7	10	13	17	3	50
	14 fish, starting in Year 3	0	0	13	17	20§	..	50
	18 fish, starting in Year 4	0	0	0	22	27	0	49
Bluegills	165 fish, starting in Year 1	20	45	59	0	..	..	124
	214 fish, starting in Year 2	0	57	77	0	..	..	134
Constant weight per acre to be harvested each year over specified period								
Bass	12 pounds, starting in Year 2	0	18	13	10	8	0	49
	16 pounds, starting in Year 3	0	0	17	13	11	0	41
Bluegills	38 pounds, starting in Year 1	317	141	106	0	..	..	564
	68 pounds, starting in Year 2	0	252	188	0	..	..	440

* Where constant number is to be harvested, data for each year under this heading given in weight; where constant weight is to be harvested, data given in numbers. Quota on original stock ceases after fifth year for bass, after third year for bluegills.

§ Not quite enough original stock present to fill quota.

Choose what appears to be a reasonable number to be harvested annually. Determine by a method similar to that of Regier (1962b) whether the first estimate was too large or too small, and make a second estimate. Evaluate the second estimate graphically, etc., until the optimum number is found.

Suppose the pond owner desires to harvest a constant total weight annually, instead of a constant number. Make a first estimate of the annual quota by weight. A logical choice would be the over-all total weight of original stock that would be harvested on the basis of a number quota (see Table 19) divided by the number of annual harvests. From this, estimate the number of fish to be harvested in Years 1, 2, 3, etc., by dividing the quota by the mean weight of fish in midsummer at ages I+, II+, III+, etc. Using these calculated numbers and the "known" natural mortality coefficient, determine graphically (or compute) whether the first estimate was too large or too small. Make a second estimate, etc., until the correct quota is found.

Data in Table 19 all pertain only to ponds stocked according to standard bass-bluegill policy in New York, i.e., 100-1,000 simultaneous. The author believes this policy has certain advantages over the non-standard policies tested in this study. The rates in the first part of Table 19 apply where the pond owner desires to spread the annual *number* of bass or bluegills to be harvested evenly over the number of years until the first year class hatched in the pond attains harvestable size. Those in in the second part of the table apply where the pond owner desires to harvest equal *weights* of each species each year.

The findings might be expected to apply to the "average" pond in the project area. Stated in another way, one would expect that one third of all the populations of bass or bluegills or both could support harvest rates at least as large as those in the model; in two thirds of the ponds harvest rates would have to be lower.

One third of all such ponds should support catches of 11 (or more) bass per acre per year starting with Year 2 following stocking and continuing through Year 5. If the pond owner preferred to forego taking age II+ bass, he could harvest about 14 per year, or 18 per year if he began fishing the fourth year. The total weight of original stock to be harvested would be about 50 pounds per acre in each case. Table 17 shows that the maximum standing crop of original bass stock, from Years 3 to 5, would also be about 50 pounds per acre.

Similarly with bluegills, half the ponds could support harvests of about 165 fish of original stock from Year 1 to Year 4. If he preferred not to take yearlings (about 5.5 inches long), the owner could remove about 214 bluegills annually starting in Year 2. Total weights of original stock removed would be about 130 pounds per acre in both cases. The total standing crop of original bluegill stock would reach a maximum of about 140 pounds per acre in Year 2 (Table 17).

Suppose the owner of an "average" 1-acre pond is interested in quotas by weight rather than by number. Table 19 indicates that 12 pounds of bass may be removed annually beginning in Year 2, or 16 pounds beginning in Year 3. Similarly for bluegills, 38 pounds may be removed annually starting in Year 1, or 68 pounds starting in Year 2. Considering total harvests (bass plus bluegills) beginning as soon as possible after stocking, 38 pounds may be removed in Year 1 and 50 pounds thereafter.

It should be strongly emphasized that these estimates are expected values. One would not expect them to apply precisely to any particular pond. Furthermore, they apply only to populations that had not suffered severe kills and that were uncontaminated with other fish species except to a negligible degree. The ponds are considered to be moderately to highly fertile with only moderate to little fluctuation in pond surface area. The estimated means would apply to perhaps two-thirds of the recently stocked bass-bluegill ponds in New York. In the other third, harvests would probably average considerably lower.

Two other estimated rates, the limiting cases, are of particular importance. One limit is the case where all fish of a species die within a year or two of stocking; in these the harvests are zero. Fortunately this seems to be a relatively rare occurrence with both bass and bluegills. However, severe kills after three or four years are not rare; in these, large bass seem to suffer greater mortality than bluegills.

The other limiting case relates to hypothetical populations in which no natural mortality of original stock occurs. This, too, is rare. With standard stocking, bass harvests could obviously be 25 per acre per year for Years 2 to 5, and bluegill harvests could be 250 per acre for Years 1 to 4. If growth rates at these higher densities were no lower than where normal natural mortality occurred, then the over-all total weight harvested in each case would be 120 pounds of bass and 300 pounds of bluegills. If quotas were in terms of weight, this would result in annual total harvests of a little over 100 pounds per acre per year, i.e., 30 pounds of bass and about 75 pounds of bluegills after the first year.

Population Condition

One aspect of the biology of these three groups of bass-bluegill populations remains to be discussed, namely population condition. Biologists working with bass-sunfish populations have grappled for some 25 years with the problems of maintaining good population condition, or "balance". Cause and effect in this respect are poorly understood at best.

Swingle (1950) examined population condition in some detail and proposed that "state of balance" be examined using the well known F/C ratio, A_T value, etc. (see Rounsefell and Everhart, 1953). For a number of reasons (Regier, 1961) this approach was found inappropriate in the

present study. Thus, rather than speak of "balance" and "ratios" the author chose to speak of "crowding" and "plumpness". If so many fish of a species are present in a pond that their plumpness is poor relative to the normal plumpness observed in ponds and or that their growth rates are low relative to the normal growth rates observed, then that population is considered "crowded". If the converse is true, the population is considered uncrowded.

The terms "crowded" and "uncrowded" are not meant to imply that one condition is necessarily more satisfactory than the other. Thus a moderately crowded population of 10- to 15-inch bass might be desirable under New York conditions. On the other hand, a heavily crowded population of 3-inch bluegills would likely be undesirable.

A clear understanding of the many factors affecting population condition cannot be gained from project data. The great variability is readily apparent in the data presented in previous sections. Many more replicates, much more time, and greater control of the many factors involved would have been required. However, the data do provide some useful information. Did plumpness of bass differ significantly between the experimental pond categories? How frequently did crowding of bass or bluegills or both occur in populations of the three categories? How may crowding be alleviated? These are discussed.

Population Condition in Three Bass-Bluegill Categories Table 20 contains a summary of findings on population condition in the three bass-bluegill categories. Bluegills showed a strong tendency, and bass a weak tendency, toward crowding, at least in simultaneously stocked ponds.

Eleven of 13 bluegill populations in the simultaneous categories became crowded from 3 to 5 years after stocking; in these categories only two of the 13 bass populations became crowded. In the seven ponds of the staggered category, two bluegill populations and three bass populations became crowded 3 to 5 years after stocking.

Differences between the two simultaneous categories in the proportion of ponds exhibiting crowding of a particular species were clearly non-significant. The differences between the simultaneous and staggered categories were more pronounced. The hypotheses that, for a given species, the tendency toward crowding was equally strong in ponds of the simultaneous and staggered categories were tested using adjusted chi-square as the criterion (Steel and Torrie, 1960). Differences with respect to bluegills were found to be significant, differences with respect to bass not. Since the test was partly dictated by the data, the chi-square value for bluegills cannot be considered conclusive so much as suggestive. Thus the evidence suggests that bluegill crowding is more common with simultaneous stocking than with staggered stocking, during the first five years after stocking.

Table 20. Summary of Authors' Conclusions on Condition of Populations in Ponds of Three Experimental Categories

Experimental category	Pond	Population condition *		
		Both species uncrowded	Bluegills crowded	Bass crowded
100-500 simultaneous.....	Arnot K-3§	0–3	4–5	..
	A. Hayes	0–4	5	..
	Barrett CC	0–2	3–4	..
	Moore	0–4	..	..
	Fell-Moser	0–2	3–4	..
	Cotton-Hanlon	0–3	4	..
100–1,000 simultaneous.....	Arnot K-2§	0–4	5	..
	Lange	0–3	4	..
	Arnot K-5§	0–3	4–5	..
	Barrett Rw †	0–1	2–5	..
	Warren I §	0–3	..	4–5
	Catherwood	0–2	3–4	3–4
	Warren II §	0–4	5	..
100-1,000 staggered.....	Beattie	0–4	..	..
	Hatchery H §	0–3, 6	..	4–5
	Baldwin	0–2	..	3–5
	Hoffman	0–4	..	..
	Alfred II	0–2	3–4	..
	Agronomy A §	0–2	3–5	..
	Foster	0–3	..	4–5

* Numbers denote years after bass were stocked.
§ Heavily fertilized.
† Seriously contaminated with brown bullheads in Year 5.

Plumpness of Bass Tables 21 and 22 contain data on the estimated mean weight of largemouth bass at 10 inches total length in bass-bluegill populations. These data are measures of plumpness. The data are presented to permit comparisons between years within categories, and within years between categories.

The estimates were made in the following manner. For a given inventory in a given pond, length and weight data were plotted on logarithmic graph paper and a straight line was fitted, by eye, to the resulting points. Almost without exception the points appeared to lie close to a straight line. The mean weight at 10 inches was then estimated from the graph, i.e., based on data for the original stock plus subsequent year classes.

Very few data on bass were available from some inventories; in such cases no estimate of weight was made. In many cases no bass approaching 10 inches long were present in a pond, but where larger and smaller bass were present the author interpolated to estimate the mean at 10 inches. Where only larger bass were present the author interpolated between available data and a point near 3.0 inches and 0.016 pound.

Table 21. Estimated Mean Weights of 10-inch Bass in Ponds of Three Experimental Categories

Experimental category	Pond	Years after bass stocking			
		2	3	4	5
100–500 simultaneous.....	Arnot K-3	0.49	0.56	0.49	0.46
	A. Hayes	0.50	0.50	0.50	0.50
	Barrett CC	0.58	0.62	0.56	..
	Moore	0.54	0.55	0.58	..
	Fell-Moser	0.50	§	0.57	..
	Cotton-Hanlon	§	0.51	0.54	..
100-1,000 simultaneous.....	Arnot K-2	0.54	0.58	0.51	0.50
	Lange	0.57	0.55	0.54	..
	Arnot K-5	0.56	§	0.52	0.52
	Barrett Rw	0.58	0.51	0.51	..
	Warren I	0.53	0.56	§	0.48
	Catherwood	0.50	0.46	0.53	..
	Warren II	0.56	0.58	0.60	0.56
100–1,000 staggered.....	Beattie	0.61	0.60	0.58	0.54
	Hatchery H*	0.58	0.52	0.50	0.53
	Baldwin	0.56	0.55	0.46	0.45
	Hoffman	0.57	0.52	0.51	..
	Alfred II	0.56	0.55	0.62	..
	Agronomy A	0.56	0.54	0.56	0.51
	Foster	0.50	0.54	0.48	0.45
	Lakemont	0.60	0.52	0.57	..

* The datum for Year 6 was 0.48.
§ No data available.

The point (3.0, 0.016) corresponds to the median weight of largemouth bass at 3.0 inches total length as estimated by Carlander (1953) on the basis of a survey of published findings on bass in various habitats. This point corresponds closely to findings in project ponds in which data from a wide range of bass sizes were available.

Carlander (1953) found that the median weight for 10-inch largemouth bass was 0.55 pound and that the range enclosing the central 50 per cent of values in published results was 0.50 and 0.57 pound. These data can be used as criteria by which to evaluate the data on plumpness in Tables 21 and 22.

The range for bass in project populations was 0.45 to 0.62 pound (Table 21). Considering 0.55 as the usual weight for largemouth bass, the range extended from 82 to 113 per cent of the mean. There was considerable variation in data even from the same year and category.

There was a noticeable trend in within-category means over the years following stocking. With the exception of an increase between Years 2 and 3 in the 100-500 simultaneous category, plumpness apparently decreased gradually from Years 2 to 5. By Year 5, bass in most bass-bluegill ponds were quite thin. Mean weight was 0.48 pound or less

Table 22. Comparison of Estimated Within-category Mean Weights * of 10-inch Bass in Two Species Combinations

Experimental category	Years after stocking			
	2	3	4	5
Bass-bluegills				
100-500 simultaneous	0.52 (5)	0.55 (5)	0.54 (6)	0.48 (2)
100–1,000 simultaneous	0.55 (7)	0.54 (6)	0.54 (6)	0.52 (4)
100-1,000 staggered	0.57 (8)	0.54 (8)	0.54 (8)	0.50 (5)
Bass-shiners §				
100-400 simultaneous	0.56 (7)	0.52 (6)	0.51 (6)	0.49 (5)

* Unweighted arithmetic means of date in Table 21; figures in parentheses represent number of ponds involved in each case.
§ From Regier (1963a).

in four ponds, in three of which (Warren I, Baldwin, Foster) bass were apparently quite severely crowded.

Differences between bass-bluegill categories within years were not pronounced (Table 22). Since the ranges about the means for each year after stocking were nearly identical, none of the differences appear to have been significant.

Similar data are not given for bluegills; by inspection the author determined that plumpness varied considerably even between ponds within categories during the same year following stocking.

Factors Influencing Population Condition According to most writers on farm ponds, population condition is influenced by size of pond, fertility, presence or absence of weeds, harvest practices, degree of natural mortality, and other factors. Project data have been examined for information on these factors.

Concerning the effect of pond size on population condition, most students of farm ponds have warned that unfertilized ponds of less than 0.5 acre, and carefully fertilized ponds of less than 0.25 acre, may be unmanageable due to the unpredictability of population dynamics. Table 20 ranks ponds from smallest to largest in each category, and heavily fertilized ponds are identified. The author concludes that the larger ponds exhibited approximately as strong a tendency toward bluegill crowding as did the smaller ponds.

Heavy fertilization neither prevented nor delayed bluegill or bass crowding, but all heavily fertilized project ponds had surface areas less than 0.8 acre.

It has often been stated that the presence of large weedy areas in a pond predisposes it to bluegill crowding because weeds provide cover and thus protect small bluegills from predation. Plants that commonly occurred in project ponds included species of *Potamogeton*, *Elodea*, *Chara*, *Typha*, and such filamentous algae as *Spirogyra* and *Cladophora*. With few exceptions, none of the ponds was ever choked with weeds. The exceptions were the Beattie pond which was choked with *Elodea* and *Cladophora* in the last two summers, and Barrett Rw pond that also contained *Elodea* during the last two summers of the investigation. The bluegill population remained very low in the Beattie pond, but in the Barrett Rw pond bluegills had become crowded before the weeds became a serious problem. Rooted aquatics were generally restricted to a 5- to 10-foot-wide border near shore in the other ponds of these categories. The following ponds usually had few weeds and probably never had more than about 10 per cent of the pond bottom covered with rooted aquatics: Agronomy A, Arnot K-2, Arnot K-3, Arnot K-5, Barrett CC, Moore, Warren I, Warren II, and Hatchery H. With two exceptions, these were the heavily fertilized ponds. Five of these nine ponds became crowded with bluegills. The available data, therefore, indicate that weediness did not necessarily lead to bluegill crowding, nor did lack of weeds prevent bluegill crowding.

Some writers have stated that bluegill crowding may be caused by harvesting too many bass. Bass harvests were quite low in project ponds with the possible exception of the Barrett CC pond. Thus, this was probably not a major cause of most instances of observed crowding.

Relatively low populations of one or both species, or complete extinction, can result from severe kills. Quite severe kills of both species occurred in project ponds as follows: Agronomy A in Year 3, A. Hayes in Year 4, Warren I in Year 3, Alfred II in Year 4, Fell-Moser in Year 5, and Lakemont in Year 4. The first three were summerkills, possibly due to inventory activities (A. Hayes and Warren I) and over-fertilization (Agronomy A); the others were winterkills. Large bass apparently suffered more severe mortality than either bluegills or smaller bass in each case. Populations were inventoried at least once a year for two years after the kills in the first three ponds; in the first two bluegills became crowded, in the last one bass became crowded. In the three ponds that suffered winterkills, bass mortality was apparently complete in the last two and severe in the first, while bluegill mortality was almost complete in the last two and quite severe in the first.

It seems likely that as ponds age and become richer the risk of severe mortality, especially from winterkill, would increase. Such a risk might

become quite large in small ponds with maximum depths of less than 8 feet, as was usually the case in warm-water farm ponds in the project area. However, subsurface seepage, where it occurs, may reduce this risk.

Some possible mechanisms leading to crowding of one or both species have been examined singly. Taken individually, none provided an explanation for the observed frequency of bluegill crowding. This does not imply that each factor did not exert some influence toward crowding; if each did exert an influence then the effects were too confounded to become apparent.

Whatever effect various environmental factors exert on population condition, the author feels that the main cause for crowding among bluegills is their great reproductive capacity. It is interesting to observe how bluegill crowding develops and intensifies. Regier (1962b) included examples of bluegill growth in the Arnot K-2, Barrett CC, and Catherwood ponds, all of which showed crowding at the last inventory dates. The data for these and other bluegill populations indicated that under crowded conditions, smaller bluegills grew more rapidly than larger bluegills. This suggests that small bluegills may be more efficient foragers than larger bluegills. Since bluegills are only mildly cannibalistic, crowded populations cannot prevent further crowding from occurring unless the crowding becomes so intense that reproduction ceases or very nearly all eggs and bluegill fry are consumed by the bluegills. Therefore, bluegills stand a very serious risk of crowding every summer in which heavy reproduction occurs unless yearling and older bass happen to be present in sufficient numbers to prey effectively on small bluegills. The danger of crowding is considerably less with bass than with bluegills, probably because largemouth bass are less prolific and more cannibalistic than bluegills.

Given an uncrowded bluegill population, if the likelihood of very successful reproduction without adequate bass predation is 1 in 4, then the chance of a particular bluegill population remaining uncrowded for n years is $(0.75)^n$. This probability is 0.42 for $n = 3$, 0.24 for $n = 5$, and 0.13 for $n = 7$. If the likelihood of a crowded population reverting to an uncrowded one is fairly low, as it appears to be, then on the foregoing assumption most bluegill populations would soon become crowded and remain so for a number of years.

Methods to Reduce Crowding It has been shown that bluegills in project ponds exhibited a strong tendency toward crowding. Project personnel removed small bluegills (usually less than 3.5 inches long) from eight crowded bluegill populations; data on these removals were presented in Table 18. How successful were these attempts at alleviating crowding?

Severe winterkill followed the removal of small bluegills in two

ponds (Alfred II and Fell-Moser), thus effects of the removals could not be determined in these two cases. Bluegills remained crowded the following year in each of the six remaining ponds; the proportion of small (less than 5.2 inches) bluegills removed from these six ponds varied from about 1/6 to 1/2. The author concludes that greater proportions of small bluegills would have to be removed to reduce crowding effectively. According to Wahl (1958) this should be done gradually in summer and autumn to prevent a compensatory burst of spawning.

Wahl (1958) discussed the use of chicken wire traps to reduce the density of bluegill populations in project ponds. The traps and methods used were not very effective with crowded populations of small bluegills.

Pond-Owner Reactions

The problem of ascertaining pond-owner likes and dislikes is a complicated one. To get highly reliable data would require the services of a specialist in opinion sampling. An impersonal, objective survey was not attempted. The available information on reactions of project cooperators consists of the author's impressions from discussions with each one and from a study of management and angling records.

Eleven private owners were involved in the bass-bluegill studies. Only one showed a strong interest in the fish populations. Nine showed mild to moderate interest and occasionally fished the pond or permitted friends to do so. One pond owner showed very little interest. All were apparently more interested in bass than bluegills.

Three of the seven Cornell ponds were on lands controlled by departments other than the Conservation Department. Bluegill harvests were large in one of these three ponds (Agronomy A), but apparently the great majority of the bluegills removed, including some over 7 inches long, were discarded on the bank. The other two ponds (Warren I and Warren II) were fished intermittently until it became known that quite a number of large bass were present in the latter, and then fishing pressure on it increased.

Apparently no cooperator was interested in the fish primarily as food, though they generally ate some or all of the fish that they caught.

DISCUSSION AND CONCLUSIONS

The findings of this investigation, as well as information in the literature on farm ponds, are considered here as they relate to the stocking and management of largemouth bass and bluegills in farm ponds in New York. The discussion concerns, first, characteristics of the ponds and their owners, and then the ecology and management of the fish.

Characteristics of Farm Ponds and Their Owners

The term "warm-water", with reference to New York ponds, has not been precisely defined in the preceding sections. It has been used to describe ponds which warm up sufficiently to permit certain eurythermous species to spawn and grow satisfactorily. However, this is still not a precise definition since what is "warm" for the golden shiner may be cold for the bluegill.

If a largemouth bass-bluegill population is to maintain itself, pond surface waters apparently must attain and maintain temperatures of 80° F. or above for a number of weeks annually to permit bluegill spawning. For the largemouth bass-golden shiner combination, or for channel catfish alone, the fish might reproduce and grow satisfactorily in ponds whose temperatures did not rise much above 70° F. Eurythermous fish species tested in this project could all, except the bluegill, maintain populations in marginal trout ponds (maximum surface temperatures of about 73° to 77° F.). Whether growth of the warm-water species would be satisfactory in New York ponds at these lower temperatures has not been investigated. The literature contains contradictory findings concerning largemouth bass growth at temperatures below 80° F. (cf. Swingle, 1949; and Wurtz-Arlet, 1952).

Therefore, warm-water ponds are those in which the particular eurythermous species under consideration can grow and reproduce successfully and satisfactorily. Thus defined, they include some in which less eurythermous species such as brook trout would thrive.

The farm ponds used in this study have been described. The author considers them to have been better built and better managed, on the whole, than ponds of this kind in New York generally. As environments for the warm-water fish tested, they probably ranged in the better two-thirds of warm-water ponds in the State. Thus, generalizations based on project findings should apply to the "somewhat better than average" ponds.

Almost all New York ponds are constructed either for recreation (swimming, fishing, skating, scenery) or as a source of stock-water or fire protection or a combination of these. The pond is usually located near the house if built for recreation or fire protection or both; if for stock-water, the pond is situated on permanent pasture and may be some distance from the farm buildings. One would expect most recreational ponds to be better managed for fish than most stock-water ponds.

Probably the two most important characteristics of ponds with respect to fish stocking and management methods are pond size and fertility. Weediness is of prime importance in itself, but is so closely related to both pond size and pond fertility that it will not be discussed separately.

Pond Construction and Size Most farm ponds in New York have areas less than 0.5 acre with many less than 0.25 acre. Maximum

depth is usually less than 10 feet, and not infrequently less than 7 feet in midsummer. Within 5 years of the construction date, perhaps 20 per cent no longer function as planned, partly because of design and construction defects and partly due to lack of proper maintenance.

A number of biologists have warned that small shallow ponds are difficult to manage for fish. Such warnings have been made concerning ponds in Alabama (Swingle, 1949), Kentucky (Hall, 1959), West Virginia (Dugan, 1956), Iowa (Hull, Wilcox and Speaker, 1950), Ohio (Davis, 1958), Wisconsin (Brynildson and Truogg, 1959), Pennsylvania (Wingard, 1955), and elsewhere. Minimum size for effective fish management is usually given as 0.25 acre if pond and fish are to be carefully managed, 0.5 acre if they will receive little management. Biologists from the more northern states usually add that the ponds should be relatively deep.

Some biologists specify minimum sizes considerably larger than 0.25 and 0.5 acre. Kennamer (1957) stated that Alabama ponds of less than 1 acre are troublesome to manage. Holloway (1951) made a survey of 612 ponds in the Southeast. He concluded that "little degree of success" could be expected from unfertilized ponds smaller than 2 acres if built on clay soils or smaller than 8 acres if built on sandy soils, unless special care were taken in pond design or some form of weed control were practiced.

The stated or implied reasons why small ponds are considered difficult to manage include: (1) small populations tend to be more unstable than large populations; (2) weeds are apt to be a more serious problem in small ponds because they interfere with normal use of the pond and provide undesired cover for small bluegills; (3) summerkill or winterkill or both are apt to occur in small, shallow, weedy ponds; (4) small ponds may not provide enough fishing to make management for fish worthwhile. The present author feels that these considerations all apply to the smaller ponds in New York. However, the first, second, and fourth points seem to be more serious with largemouth bass and bluegills than with largemouth bass and golden shiners, for example.

The figures 0.25 and 0.5 acre seem rather arbitrary. On what basis were they set? One approach would be to estimate both costs (including risks) and benefits of constructing and managing ponds of various sizes and then determine at what minimum sizes ponds cease to be economical. The problem is obviously formidable and apparently no one has attempted it. Likely the limits 0.25 and 0.5 were set on the basis of "educated guesses". On a similar basis the present author feels that 0.5 acre as the lower limit for New York ponds that are not intensively managed is too high, at least for bass-shiner ponds. But 0.5 acre may be a fair lower limit for bass-bluegill ponds.

Pond Fertility According to Swingle (1947) proper fertilization serves a number of purposes in southeastern ponds: (1) properly fertilized

ponds have approximately uniform carrying capacities, permitting use of standardized stocking and management methods; (2) addition of certain inorganic ions results in increased rates of fish production; persistent plankton blooms result when ponds are properly fertilized, and the plankton is a link in the food chain of fish; (3) plankton blooms shade out pond weeds, i.e., submergent and emergent rooted aquatics and filamentous algae; such weeds affect adversely both fish population dynamics and pond uses such as fishing, boating, swimming, etc. Each of these may be examined with respect to pond conditions in New York.

The necessity for uniform carrying capacities followed from Swingle's emphasis on proper stocking rates of bass and bluegills to increase markedly the chances of long-term population balance (Swingle, 1950). Whether these stocking rates and ratios do exert a long-term influence in northern ponds fertilized and managed *exactly* as recommended by Swingle is not known. They do not seem to exert such an influence in ponds fertilized and managed *approximately* in the Swingle manner. (cf. Krumholz, 1950.)

Evidence from this project on the relationship of fish production rates to the rate of fertilization is not clear-cut. Data were presented showing that higher standing crops of bass and bluegills tended to occur in those ponds receiving relatively large amounts of inorganic fertilizer. This relationship was not apparent with other species and species combinations, possibly because of inadequacies of the data.

Heavy fertilization tends to control rooted aquatics but not filamentous algae in New York ponds. Thirteen project ponds were heavily fertilized for at least four consecutive years and only one (a shallow, leaky pond) became seriously weedy. Almost all of the ponds that were less heavily fertilized had more extensive stands of rooted aquatics. The one clear-cut exception was a pond kept highly turbid with suspended clay from cattle tramping. However, the fertilization that tended to control rooted aquatics seemed less effective with filamentous algae of the genera *Spirogyra* and *Cladophora;* the latter not infrequently formed extensive floating mats on both fertilized and unfertilized ponds.

Perhaps the reason why fertilization seems to control weeds more effectively in Alabama ponds (near Auburn) than in ponds in central New York is connected with differences in water chemistry. Swingle's fertilization experiments were conducted in ponds located in the southern Piedmont, where runoff and ground waters are very soft. According to Surber (1949) and Ball (1949), weed control by fertilization seems to be less effective in the hard waters of West Virginia and Michigan than in the soft waters of Alabama. Surber gave the following explanation:

> "Hard-water ponds are likely to remain clear or will clear up more rapidly than soft-water ponds because of the chemical processes which take place in the water. In limestone regions, large quantities of bicarbonates present in the water are broken down by plants, forming precipitates which serve to carry to the bottom suspended materials drifting in the water. This is not true of soft waters where there is little bicarbonate or other mineral compounds to be broken down by plant activity."

Forney (1957b) found considerable diversity in the chemical characteristics of New York farm ponds. He found that in 48 ponds total alkalinity ranged from 5 to 226 ppm and total dissolved solids from 50 to 420 ppm. If Surber's explanation is correct, then Swingle's method of fertilization might control weeds satisfactorily in soft-water ponds in New York.

Swingle and Smith (1942a) stated that the presence of weeds predisposed bass-bluegill populations to bluegill crowding due to cover afforded young bluegills. Holloway (1951) concluded that ponds in the Southeast should have no more than 10 per cent of their area covered with weeds if the chances of balance were to remain good.

Seven very fertile bass-bluegill ponds used in the present project contained few or no emergent or submergent higher plants. Bluegills became seriously crowded in five of these within 5 years of stocking, and bass were crowded in the remaining two. In the three ponds in which infestation with rooted aquatics and filamentous algae was lowest, bluegills nevertheless became crowded. Thus, almost total absence of weeds in a bass-bluegill pond in New York is no guarantee that overcrowding of one or both species will not occur.

So far this discussion has involved an examination of Swingle's reasons why ponds in the South should be heavily fertilized. The present author has shown that it is at least doubtful whether proper fertilization of ponds in New York would lead to the desired effects with satisfactorily high probability. There are a number of possible reasons why heavy fertilization should not be recommended.

1. Fertilization increases the rate at which organic material accumulates in ponds. Farm ponds in New York are usually quite small and quite shallow, they are ice-covered for about 4 months each year, and winterkill is a constant risk. Fertilization very likely increases the risk of winterkill. Dense plankton blooms following fertilization may also cause summerkill occasionally, by exhausting oxygen during warm nights following overcast days.
2. A certain amount of rooted aquatics, far from being an unmitigated nuisance, may actually be desirable in many New York ponds. The golden shiner apparently requires aquatic vegetation on which to spawn. Also the higher plants become a suitable environment for larger aquatic insects that serve as food for both small and large bass.
3. There are psychological and aesthetic reasons why some pond owners prefer not to fertilize their ponds heavily. Many that swim in farm ponds are repelled by the pea-soup appearance of a heavy phytoplankton bloom. Others find a combination of high water transparency, cattails, spikerush, pond lilies, and fish more pleasing aesthetically than a pond containing a relatively opaque plankton mixture and little or no emergent vegetation.

4. Fertilization takes time and costs money. Many pond owners in New York are not particularly interested in producing the highest possible yields of fish. Many would feel that increased fish production was not worth the time and money required for the necessary fertilization program.

For one or more of these reasons, biologists in a number of states have decided not to recommend intensive fertilization: Illinois (Bennett, 1952), Indiana (Krumholz, 1950), Iowa (Carlander, 1952), Ohio (Davis, 1958), Michigan (Ball, 1952) and Wisconsin (Brynildson and Truogg, 1959), among others. The present author does not recommend intensive fertilization for New York ponds generally. If the owner of a larger, deeper pond containing bass and bluegills seriously intends to produce the best possible bluegill fishing, then he should probably fertilize intensively. Under New York conditions intensive fertilization would require annual additions of about 1,000 pounds of fertilizer containing 8 percent phosphorus pentoxide.

With respect to fertilization of trout ponds in New York, Eipper (1960) stated:

> "One application of inorganic fertilizer at a rate of 300 pounds per acre can be applied to a newly-dug pond as it is starting to fill. This practice appears to be safe, and although not a necessity it may somewhat hasten the establishment of a natural food supply in new ponds."

Probably newly dug ponds intended for warm-water species would also benefit from application of 300 to 500 pounds per acre for the first year or two. A convenient and satisfactory method of applying fertilizer is to cut a large rectangular window in the side of the fertilizer bag and carefully lower the bag, window up, into 2 feet of water in the windward corner of the pond.

To summarize briefly, intensive fertilization is not recommended for New York ponds generally, but may have its place in exceptional ponds. Proper fertilization may control submergent and emergent weeds, but may not control filamentous algae. It likely increases fish (particularly bluegill) production in bass-bluegill ponds, but it may have little effect or may even decrease bass production in bass-shiner ponds. Heavy fertilization increases the risk of winterkill and summerkill. Some pond owners find dense blooms unpleasant when swimming; aesthetically some prefer a moderately weedy pond to a heavily fertilized weedless pond. Intensive fertilization takes more time and costs more money than many New York pond owners, interested only in obtaining moderate amounts of sport fishing, can justify.

Pond-owner Characteristics The discussion in the preceding section has implied that pond-owner preferences and practices must be taken into account in formulating pond stocking and management policy. This is so obviously the case that it is almost pointless to state it. How-

ever, it is surprising how seldom these preferences and practices are explicitly taken into consideration in the literature on farm ponds.

Personnel of this project did not undertake an actual survey of pond owners in New York to determine their preferences and practices with respect to farm fish ponds. They were, however, in fairly close contact with project cooperators, Cornell Extension Service biologists, Soil Conservation Service biologists (on both regional and district levels), county agricultural agents, and State Conservation Department biologists. Following are the author's conclusions based on information from those sources.

Pond owners usually desire ponds for a number of reasons one of which is fishing. If management for fish interferes with some of the other uses, as intensive fish management may, then such fish management may not be practiced.

Some writers have stated that bass-bluegill ponds should be fished at rates of 500 hours per acre per year, or more, for maximum fish production. Such recommendations have been made for West Virginia (Dugan, 1956), Pennsylvania (Wingard, 1955) and Ohio (Davis, 1958). Few, if any, farm ponds in New York are fished at anything approaching this intensity. Most are not fished intensively, i.e., apparently less than 50 angler hours per acre per year in most cases. In relatively few ponds does it rise to 100 hours, and in many it does not average above 25 hours per acre annually.

Some New York pond owners are avid fishermen. But almost all have access to good fishing in natural waters near their homes, and most have a number of good fishing waters from which to choose (Regier, 1960). In some of the southern states the alternatives to farm-pond fishing are more limited, and this may explain the greater interest in intensive pond management for fish in those states.

What type of fishing do New York pond owners prefer? Most prefer fishing for largemouth bass to that for bluegills. In fact, project personnel and Cornell Extension Service biologists have encountered few avid bluegill fishermen in the State. This may be contrasted with the following statement by Dickson (1955) concerning Georgia pond owners (bream is a common name for bluegill in the South):

> "Three to 5 pounds of bream should and can be caught for each pound of bass. Most pond owners need not worry about fishing each species properly as there will be approximately 20 bream fishermen for every bass fisherman."

Swingle (1950) found that pond fishermen in Alabama considered the minimum harvestable size to be 0.1 pound for bluegills and 0.4 pound for bass. Few pond owners in New York consider 0.1-pound bluegills harvestable and most are only interested in bluegills that have reached about 0.25 pound (6.5 inches). Most of them also consider a 10-inch

bass (about 0.55 pound) as the minimum harvestable size, perhaps because this has been the lower legal limit for many years. The author feels that it would be a difficult task indeed to interest New York pond owners in bluegills smaller than 6.5 inches. However, they could probably be induced to fish for smaller bass if this were desirable, as it probably is on occasion (Regier, 1963a).

In summary, it seems that the great majority of New York's warmwater pond owners desire a moderate amount of good sport fishing, preferably with a minimum of management.

General Management of Farm Ponds

About two million farm and ranch ponds had been built in the United States by 1958 according to Hagen and O'Connor (1959). Probably most of these were stocked with fish provided by government agencies. The species most frequently used were largemouth bass and bluegills. The evolution of some pond stocking policies and management recommendations has been discussed by Regier (1962c).

Biologists in a number of midwestern states have recommended during the past decade that bluegill stocking in those states should be drastically reduced. This is also the present author's conclusion concerning bluegill stocking in New York ponds, for reasons summarized here. The author feels that the golden shiner should be stocked instead of the bluegill in many New York ponds, for reasons given elsewhere (Regier, 1963a).

Pond Studies Cornell fishery biologists have studied fish populations in New York ponds for over 10 years. The findings, important as they may be, are nevertheless quite sketchy. Only a limited number of species in a limited number of combinations and rates were tested for a limited number of years in a limited number of ponds in a limited part of the State. It is hazardous to generalize on the basis of such studies. This is emphasized by the extreme variability in farm-pond fisheries data as well illustrated in the present study and others, e.g., Hall (1959) and Holloway (1951). On the other hand, these studies have been far more comprehensive than any other pond studies in the northeastern United States. Thus, if stocking and management recommendations for New York are to be based on scientific studies made in environments similar to those in New York farm ponds, then they must be based largely on these findings.

Long-term farm-pond investigations have been in progress in Alabama and Illinois. Quite comprehensive studies of shorter term have been conducted in Indiana, Michigan and Kentucky. The results of this work may be used to supplement the findings of the studies in New York to the extent that pond conditions and pond-owner preferences and practices in this State resemble those in other states.

Choice of Species There are a number of warm-water fish species that can survive and reproduce in New York farm ponds. There are a larger number of combinations of such species that, if stocked, would survive and reproduce. On what basis are particular species or combinations chosen for a widespread pond-stocking program? The following five principles may serve as criteria.

1. The species must be popular for sport fishing or must serve satisfactorily as prey for game fish, or both. Very few American pond owners are interested in a food fish that is not sporty to catch.
2. The species must survive, grow and, preferably, reproduce satisfactorily in the type of pond where they are to be stocked.
3. The species must be such that they would not seriously interfere with fisheries in local natural waters into which they might escape from the pond.
4. Stock must be readily available. In the context of presently accepted practices this usually means that government agencies are either currently rearing young of these species or could do so without a major change in facilities or finances. But stock may also be available locally, either from private fish hatcheries, from bait-fish dealers, or from natural waters if removal therefrom is legal.
5. Costs of stocking and managing the species must be less than benefits derived from the stocking and management. Costs must also be less than the cheapest alternative method of providing the pond owner with equivalent fishing. At present the policy of government agencies is apparently to keep the number of species involved in pond-stocking programs as low as possible; this leads to minimum costs of propagation and distribution.

It was on the basis of these considerations that the species used for these experiments were chosen. Findings in this and other states suggested that largemouth bass, bluegills, channel catfish, and golden shiners would meet all the above criteria. Exploratory investigations were also undertaken with smallmouth bass, black crappies, yellow perch, chain pickerel and fathead minnows (Regier, 1961).

Choice of Stocking Rates What are the considerations that determine the rates at which fish should be stocked? There are at least three sets of criteria available; these may be stated as follows within the context of bass-bluegill stocking, but they apply with little modification to other combinations.

1. Based on writings by Swingle with respect to conditions in Alabama (see Swingle and Smith, 1947; and Swingle, 1950):
   (a) Rates should be such that the original stock should grow fairly rapidly.

(b) The fish population's biomass should increase rapidly until it reaches the carrying capacity of the pond.
(c) The fish population should attain balance.

2. Krumholz (1952) proposed that, for Indiana ponds, only enough individuals of each species should be introduced to get the population established.
3. The present author agrees with Krumholz (*op. cit.*) that long-term stability (or balance) in a bass-bluegill population is not closely related to the rates and ratios used. But he agrees with Swingle that the carrying capacity should be filled as quickly as possible and largely with fish of the original stock. In bass-bluegill ponds in New York the original bass and bluegill stock must support the fishing for at least the first five and three years, respectively. In order to achieve the greatest harvests the maximum number of each species should be stocked, subject to the condition that growth rates and plumpness remain acceptable to the pond owner.

Management Methods The author is convinced that farm-pond management methods must be simple or most pond owners will not practice them. To a fishery biologist used to thinking of fishery management problems in lakes, reservoirs, estuaries, etc., any type of farm-pond management may seem simple. But it is in the context of what pond owners know about pond ecology, and particularly fish population dynamics, that management methods must be simple.

There is also a danger of oversimplifying recommendations. The author considers that the recommendations by some writers, that the pond owner wait until both bass and bluegills have spawned and then fish as much as possible, is oversimplified. Also, if management methods are time consuming (even though simple), then the average pond owner in New York will likely find a less tiring hobby than pond management and fishing.

With these general considerations in mind, the ecology and management of the bass-bluegill combinations may be examined.

Ecology and Management of Largemouth Bass and Bluegills

A number of bass-bluegill stocking formulae (i.e., rates and ratios) have been recommended for different states or regions. Some biologists have recommended adding a third or fourth species such as redear sunfish, crappie, rock bass, channel catfish, and mosquitofish. Lagler (1952) summarized some of these more complex formulae. The present author considers reasonable a policy by government agencies that restricts the number of species provided for stocking small ponds. Therefore, this discussion is largely limited to two-species formulae.

Bass-bluegill populations in these categories are discussed with re-

spect to population dynamics, possible harvest rates, and stocking and management methods and costs.

Population Dynamics All the dynamic processes investigated (i.e., survival, growth, reproduction, production, etc.) exhibited considerable variability both within populations between years and within categories within years. Although little further reference will be made to this variability, its existence should nevertheless be borne in mind.

Means were estimated for within-category survival rates in the absence of fishing mortality. Differences between category means appeared to be insignificant in the case of bass. The over-all mean survival in the absence of fishing was about 80 per cent.

When both bass and bluegills were stocked in the same summer or autumn, bluegill survival rates were about 70 per cent per year. Predation by original bass fingerlings on original bluegill fingerlings in ponds stocked simultaneously was apparently negligible, even when the bass were large enough to swallow the bluegills. In ponds stocked with bluegill fingerlings the year following bass stocking, bluegill survival in the absence of fishing was about 25 per cent for the first 15 months, and 70 per cent per year thereafter. The high mortality of bluegills during the first 15 months in ponds where stocking was staggered was probably due to bass predation.

In Alabama, Swingle and Smith (1942b) stocked experimental ponds at rates of approximately 1,500 bluegills and 100 bass per acre. The fish were introduced as fingerlings with bluegills being stocked in late summer and bass the following spring. Under these conditions Swingle (1950) found that about 70 per cent of the bass and 75 per cent of the bluegills survived for the first year following stocking. These findings are quite similar to those for this project.

Most original bass in most of the project ponds attained minimum harvestable size (10 inches and about 0.55 pound) about midsummer in the second year following stocking. Between-category differences in growth rates were not large.

Growth rates of original bluegills ranked in inverse order to the number surviving, suggesting that their growth rates may have been density dependent. Most original bluegills in all categories attained harvestable size (about 6.5 inches and 0.25 pound) during the second summer following stocking.

The observed growth rates in moderately to very fertile ponds in New York are considerably slower than those considered to be minimum acceptable rates by Swingle (1947) in Alabama ponds. He stated that bluegills should attain a size of 0.25 pound and bass a size of 0.75 to 1.0 pound within 1 year after stocking. It seems clear that bass and bluegill growth rates are much slower in New York ponds than in Alabama ponds.

Strawn (1961) and Kramer and Smith (1960) found that growth rates

of age 0+ largemouth bass were directly correlated with water temperature. Thus slower growth of bass in New York ponds as compared with that in Alabama ponds may be due largely to temperature-related differences between ponds of the two regions.

Original bass generally first reproduced at age II+, original bluegills at I+. Reproduction of both species occurred fairly regularly after the initial spawning. During the first two years after stocking, bass reproduction was apparently more successful and bluegill reproduction less successful with staggered stocking than with simultaneous stocking. These differences were apparently not maintained beyond the first two years.

Bass and bluegills in Indiana, Kentucky and Michigan ponds usually first reproduce at the same ages as those in New York ponds (Krumholz, 1950; Hall, 1959; Ball, 1952). In Alabama bass usually first reproduce at age I+ and bluegills may reproduce at 0+ (Swingle and Smith, 1943).

Young-of-the-year bass in project ponds apparently did not prey seriously on bluegill young-of-the-year. Bluegill and bass reproductive success was not seriously affected by crowded bluegill populations. If generally true, these findings indicate that only the yearling and older bass in a pond can prevent bluegill crowding. If such bass are not present in sufficient numbers, bluegill crowding may be quite certain to occur. And it seems that older bass are all too frequently not present in sufficient numbers.

The size of a bass-bluegill population frequently did not increase regularly to reach the carrying capacity of a pond. In some ponds increases seemed delayed for a number of years and then rapid increases occurred. Such explosions occurred considerably more frequently with bluegills than with bass. The large number of subharvestable bluegills resulting from such an explosion usually became the major component by weight of the fish population.

The more fertile project ponds tended to support higher standing crops of bass and bluegills than the less fertile ones. Total standing crops of bass were quite similar in all categories during the first three years following stocking; after that they were somewhat higher in the staggered populations than in the simultaneous populations. Differences between total standing crops of bluegills in the three categories were not marked, possibly due partly to the great variability that was in turn partially the result of bluegill population explosions.

Differences in standing crops between categories, if they occurred, were associated with very unequal harvest rates between years (following stocking) within populations, between populations within years, and between categories within years. An analysis of models of unfished original stocks indicated that standing crops of original bass were approximately equal in all categories up to 5 years after stocking. The situation

was different for bluegills, where standing crops of original stock were larger for the 100-1,000 simultaneous category than those for the 100-500 simultaneous category which were in turn larger than those for the 100-1,000 staggered category.

The average harvests in project ponds were quite light. Under the prevailing conditions, total standing crops of bass increased from an average of 40 pounds to one of about 70 pounds per acre from 2 to 5 years after stocking. Total standing crops of bluegills increased from about 100 to 250 pounds per acre over the same period.

Bluegills showed a stronger tendency toward crowding than did bass, at least in simultaneous categories. There was evidence that a tendency toward bluegill crowding was more pronounced following simultaneous stocking than staggered stocking. Almost all bluegill populations became crowded within 5 years of simultaneous stocking.

Summarizing briefly, the salient points with respect to bass-bluegill populations in farm ponds in New York are: (1) fairly slow growth rates of original stock and slower growth rates for year classes hatched in the ponds; (2) usually adequate or more than adequate reproduction of both species; (3) absence of natural ecological checks to prevent bluegills or bass or both from becoming crowded and stunted.

NUMBERS OF ORIGINAL STOCK AVAILABLE FOR HARVEST Bass-bluegill populations begun with any of the three stocking formulae used in this study could apparently have supported approximately equal bass harvests. These harvests could have averaged about 11 original bass per acre per year beginning the second year after stocking and extending through the fifth.

During the first three years after stocking, however, potential bluegill harvest rates apparently differ considerably depending upon the stocking formula used. Thus the 100-1,000 simultaneous stocking method produced average potential harvests of about 165 bluegills per year starting 1 year following stocking. This is about twice as large as with 100-500 simultaneous and three times as large as with 100-1,000 staggered stocking.

Composition of bass-bluegill populations seemed to be quite similar in all categories 4 or more years after stocking. Perhaps staggered populations would have fewer cases of bluegill crowding and more of bass crowding than simultaneous populations, and, if this is the case, then staggered stocking may have an advantage over the simultaneous stocking in this respect. On the other hand, bluegill harvests would usually be higher in the 100-1,000 simultaneous than in the 100-1,000 staggered category. The author feels that the probability of higher potential harvests outweighs the probability that bluegills will become crowded somewhat more frequently in a 100-1,000 simultaneous population.

In a recent survey of fishing in 1,000 farm ponds in various parts

of the country, King (1960) found that pond owners removed 54 original bass per acre on the average during the first year of fishing (i.e., bass of age II+). Stocking rates had varied from 50 to 100 per acre. King concluded:

> "Since it will be 1 to 3 years before a new crop of bass is produced and is available to the angler, the bass harvest may be too heavy in many ponds during the early years to keep the pond in balance. Since bluegills tend to over-populate a pond to their own detriment, as well as to that of the bass, adequate numbers of bass are required to maintain a satisfactory balance. An unbalance of this nature could be an underlying cause of poor fishing in later years."

Though high rates of bass harvest may predispose a population to bluegill crowding, the author feels that this is not the chief reason why so many bass-bluegill ponds become crowded with bluegills. Most bass-bluegill ponds studied in this project became crowded with bluegills in spite of relatively low bass harvests.

There is another aspect to the high bass harvest rates reported by King (1960). Pond owners who remove over half the original stock in the first year of fishing will certainly have poorer bass fishing the next summer and possibly the next two summers, even if bluegills do not become crowded as a result. Pond owners primarily interested in bass may then lose interest in managing the pond.

But pond owners have been urged to fish their ponds heavily. Thus Edminster (1947)[7] of the Soil Conservation Service stated:

> "The rules for deciding when to begin fishing a newly-stocked pond are simple. Rule 1: defer fishing of each species until some of them have spawned successfully. Then the future supply is assured and the breeders can safely be taken. Rule 2: take any and every fish that is worth keeping.
> "Once fishing for either species has begun it should be continued at every opportunity for the rest of the year. . . . But it is true that *you can't overfish a good well-managed pond*. . . . The real danger lies in *failing* to fish the pond enough."

Davison (1953), also of the Soil Conservation Service, made somewhat different recommendations:

> "*All the bluegills and bass you stock* from the hatchery *should be left in the pond until both bluegills and bass have spawned successfully. The mistake of fishing the bluegills after they have spawned but before the bass have done so too is commonly responsible for a serious decline in fishing success after a single year of excellent sport.*"

The reason stated for recommending that fishing for bluegills should not be done until the bass have reproduced is that the high standing crops of adult bluegills compete with small bluegills for forage and thus control the numbers of smaller bluegills. Evidence from the present study has shown that high standing crops of adult bluegills in New York ponds did not prevent further reproduction and survival of young and thus failed to prevent further bluegill crowding, probably because small blue-

[7] In this and subsequent quotations, the italics are those of the original author.

gills may be more efficient foragers than large bluegills. Davison continued:

> "It is well to catch about half the bass the second summer and fall. With extraordinary hard fishing you can remove more than that, and you will not upset your fish population seriously if you do."

Dugan (1956) carried the argument a step further.

> "*The harder the pond is fished, the more it will yield, and the larger the fish will grow.*
> "But isn't there a danger of removing too many? No, if you stick to hook and line fishing. Experiments have proved that it is impossible to overfish a farm pond unless fish are taken out with seines, dynamite, poison, or some similar means. The reason for this is quite simple. When there is severe competition for the food supply in a pond—that is, when the fish are crowded—the fish bite readily, and fishing is good. But as soon as enough fish have been removed to relieve competition for food, the remaining fish are well-fed and hard to catch. Thus they automatically protect themselves. . . ."

Perhaps the quoted statements by Edminster, Davison and Dugan are applicable to large, well-fertilized, carefully-managed ponds in the South. They do not apply to the smaller, less-well-managed ponds in New York.

The author feels that New York pond owners should try to distribute harvests of original stock more or less evenly over the years until the first year class spawned in the pond reaches harvestable size. The quotas given in Table 19 should be fairly reliable guides for the average farm pond in New York. If these were widely adopted here, about half the ponds would then be overfished and half underfished. Likely neither the overfishing nor underfishing would be severe in the majority.

In most ponds the quota system would assure the presence of adult fish to reproduce. It would usually assure a stock of large bass to keep up predation pressure on small bluegills and bass, though this predation pressure in itself would usually not be enough to prevent bluegill crowding. The presence of larger fish would also serve to maintain the interest of the pond owner in the fish population and might increase his incentive to manage the pond properly for the fish.

Management Methods and Costs According to standard bass-bluegill instructions (Swingle and Smith, 1942b; Edminster, 1947; Davison, 1953; Dugan, 1956; etc.) the important steps in managing bass and bluegills are proper pond construction, proper fertilization and proper stocking. Unfortunately the criteria by which construction and fertilization are judged to be proper exclude most New York ponds. What, then, can be done to manage bass and bluegills in New York ponds?

The author feels that even in the best-constructed, best-fertilized 10 per cent of warm-water ponds in New York, bluegills will tend to become crowded. Either the bluegills must be somehow prevented from realizing their full reproductive potential or populations of small bluegills must be reduced. Perhaps this can be done by methodic destruction

of bluegill nests, or by intensive seining of small bluegills late in summer when reproduction has been very successful. Use of chicken-wire traps (Wahl, 1958) might serve to reduce high populations of intermediate bluegills to permit more rapid growth of the remaining fish.

The author agrees that weeds are probably detrimental to bass-bluegill ponds in that they provide undesired cover for small bluegills. However, lack of cover in itself is no guarantee that bluegills will not become crowded. Weed control will continue to be a serious problem in bass-bluegill ponds in New York. Larger, deeper ponds might be fertilized heavily to shade out most higher plants. If mats of filamentous algae result, they may have to be destroyed chemically or removed mechanically. Perhaps chemical or mechanical weed control is the only safe method in the smaller, shallower ponds because of the danger of winterkill if they were fertilized heavily.

According to an analysis of farm-pond costs (Regier, 1961) managing existing larger, deeper, properly-maintained New York ponds for bass and bluegills costs about $40 per acre per year. If a pond owner built a pond exclusively for bass-bluegill fishing and planned to pay the total costs of construction, stocking and management in equal payments over 20 years, then his annual costs would be about $30 + 200A$, where A denotes area in acres and costs are in terms of 1961 dollars. It would pay such an owner to build and manage the pond only if he could not get equivalent fishing satisfaction in natural waters at an equivalent expense.

On the basis of these considerations, the author believes that the bass-bluegill combination should be stocked in New York only where a pond and its owner satisfy most of the following criteria:

1. The pond is fairly large (over 0.5 acre) and deep (over 10 feet) with steeply sloping banks all around. Its surface waters rise above 80° F. for periods of several weeks each summer.
2. Weeds will be controlled either by intensive fertilization or by chemical and mechanical means.
3. The pond owner or members of his family have a genuine interest in fishing for bluegills as well as bass.
4. The pond owner is prepared to learn and practice the latest management recommendations. This would likely involve close observation of the pond, the fish population, and harvests, as well as undertaking corrective measures when he finds these necessary.

Probably any combination of two of these four criteria would serve to exclude a majority of the warm-water farm ponds in New York.

Concerning bass-bluegill stocking formulae, neither the findings of this investigation nor those of biologists in other states have shown clearly that the standard New York bass-bluegill stocking policy (i.e., 100 bass

fingerlings and 1,000 bluegill fingerlings stocked in the same summer) should be changed.

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REPRODUCTION, GROWTH, AND MOVEMENT OF MUSKRATS INHABITING SMALL WATER AREAS IN NEW YORK STATE[1]

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ABSTRACT

Reproduction, growth, and movement activities of muskrats in 41 small water areas of central New York were studied the year around from February 1957 through July 1959. Information was secured from more than 700 muskrats, primarily through live-trapping. The onset of breeding was highly correlated with the beginning of spring movement. No indications of precocial breeding were present in 37 immature females examined in the fall. Two adult females, bred in captivity, produced litters of six and three young after gestation periods of 28 and 29 days, respectively. Adult females from the study area averaged approximately 6.3 young per litter and nearly 1.5 litters per year. The sex ratio in 174 nestlings was 105 males to 100 females; in 279 September-trapped immatures it was 118 to 100; in 228 adults trapped from July through October it was 93 to 100. The age ratio in 364 September-trapped muskrats was 328 young per 100 adults, or 5.9 young per adult female.

Fifty-three young muskrats were born and raised in captivity. Growth curves were plotted through 50 days of age. Growth rates of captive and wild litters were compared. Second-year adults, as a group, were much larger than first-year adults. Adult males generally were larger than adult females.

Movements of muskrats were studied during spring, summer, and fall periods. The spring movement was by far the most extensive and appeared to be triggered by the break up of ice on the ponds. Summer and fall movements occurred at a much lower intensity than spring movements.

Summer home ranges of adults were studied on a small marsh in 1958. Twenty-one adults were present. Home ranges of 10 males coincided with those of 10 females to such an extent that pairing was indicated. Home ranges averaged approximately 200 feet in diameter. The ranges of several "paired" adults overlapped slightly.

Homing data were obtained from 19 ear-tagged, immature and adult muskrats released one or more times at various distances and directions from home ponds. Eleven returned once. One muskrat returned five times; his longest return was 4,800 feet overnight.

Detrimental burrowing activities of the muskrat (*Ondatra zibethicus*) often outweigh the animal's value as a furbearer. Small water impoundments are particularly vulnerable to damage. The incidence and severity of muskrat burrowing damage has increased along with the constantly increasing number of impoundments. Much information is available concerning the muskrat, but few attempts have been made to study populations intensively on a continuous, year around basis. Also, much of the data in the literature supports only tentative conclusions. An intensive, continuous study was made from February 1957 through July 1959 to obtain information on reproduction, growth, and movement activities of muskrats inhabiting small water areas of central New York State as a guide to effective means of control.

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[1] A contribution of Federal Aid in Fish and Wildlife Restoration Project W-77-R. The work was supervised by W. Robert Eadie, Department of Conservation, Cornell University, to whom special thanks are extended for guidance and aid in preparation of the manuscript.

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Two areas, both located near Ithaca in Tompkins County, were selected for study. Area "A" contained 10 potholes, ponds, and small marshes ranging in size from 1/10 acre to about 1¼ acres. This was used as a pilot area early in the study and later as an experimental area. Area "B", considerably larger, was used as the main study area and was disturbed as little as possible until the last few months of the study. It included 31 potholes, ponds, and small marshes ranging in size from less than 1/10 acre to about 8 acres. Nearly all of the small water areas studied were artificial impoundments of recent origin, and were scattered throughout approximately 9 square miles of slightly rolling farmland, abandoned farmland, and patches of woodland. All were inhabited by muskrats at least at some time during the period of study. Water levels remained rather constant on most of the small marshes and ponds.

PROCEDURE

Most of the data were gathered through an intensive live-trapping, tagging, releasing, and recapturing program. Steel-trapping was used as a supplementary method off the study areas, and as a means of collecting final data on the experimental areas at the close of the study. Captive, penned muskrats were raised to obtain information on growth and reproduction.

Live-trapping Methods

Live-trapping techniques were used throughout the year. However, this procedure was greatly curtailed from December through February each winter because of difficult weather conditions. Havahart, National, and Gibbs live traps, of muskrat size, were field tested early in the study. On the basis of these tests the National trap was selected because of more positive door action, safety to the captive muskrat, and superior handling ease. The National model used was a double-spring door, cage-type, folding live trap measuring 6x6x24 inches and constructed of 1-inch-grid welded wire. Other investigators (Aldous, 1946; Shanks and Arthur, 1952) successfully used the National trap.

The selection of and spacing between trap sites differed according to the trapping purpose. For quick inventories or sampling, traps were set at such optimum trapping sites as freshly used feeding stations and defecation posts and in close proximity to active houses and burrow systems. For a more complete inventory of muskrat populations, and for home-range studies, traps were placed at fresh muskrat sign or at intervals of 25 feet if no sign were present. Traps were set also on floating platforms in order to ascertain better the extent of muskrat activity in open water, but the majority of sets were made in the manner described above. Traps were covered with grasses or pond vegetation to provide

captured animals protection against inclement weather. This procedure substantially increased the effectiveness of the trapping technique.

Early in the study apples, carrots, cabbage, potatoes, sweet potatoes, and commercial lures were compared as baits in pen tests and field tests. Carrots and apples were highly superior in acceptance. Since carrot baits showed slightly greater effectiveness than apples, and had far greater durability, especially during the warm months (the intensive live-trapping period), they were used almost exclusively in live-trapping operations. Trials with pre-baiting techniques indicated that the time expended in carrying out the procedure cancelled any value. A limited amount of bait was used at each set in order to minimize the attraction for other small mammals. Traps were rebaited each day during hot weather, and every other day during cool periods if baits were untouched.

Traps were checked daily, usually during the midmorning hours. Checking during the hours of dawn was avoided since some muskrats were active at this time. In periods of extreme cold, heat or rain, traps were visited early in the morning to minimize possible harm to the captive. Generally, traps were reset or moved immediately after checking or handling captives. Sets were usually run for 3 consecutive days and then moved if no muskrats were taken. Additional trap nights at the same site were seldom fruitful if the first three nights were unsuccessful. However, for home-range information more trap nights at the same site were sometimes required.

Live-trapping Success

Live-trapping success exceeded expectations. It was evident from retrapping information and from experiments with control methods that 100 per cent success, or very nearly so, was attained on areas intensively trapped to obtain a complete inventory of muskrat populations. Most of the animals were rather readily trapped, but variation among individuals was noted in regard to ease of recapture. One individual was captured on eight consecutive nights at three of 20 trapping stations on one pond. Five other muskrats residing on the same impoundment were captured only one to three times during the 8-day period. Many less extreme though similar incidents were observed. Differences in ease of retrapping were also evident according to the age and physical condition of the muskrat and the season. Young muskrats and sick individuals were very easily trapped and retrapped; subadults and adults generally were readily trapped, but they were somewhat more difficult to recapture than the other groups. In general, males were most easily live-trapped from late March to early May, whereas females were more easily taken in late summer or early fall. Data revealed that males are most active and wideranging in the spring, while females tend to be more active and

venture from their burrow system or house more frequently in late summer and early fall periods.

Weather conditions directly influenced trapping success. Warm, clear nights provided optimum results. (Warm as used here indicates temperatures above those of the preceding two or three nights.) Cold, wind, or heavy rain greatly reduced trapping success, apparently by curtailing normal muskrat activities. When these factors occurred in combination during any trap night, poor trapping results invariably resulted.

Trap malfunctions averaged less than one per 100 trap nights during the study and had little total effect on the data since they occurred so rarely. Serious interference with live-trapping procedures was experienced each spring and summer because of bait stealing by small rodents. Occasionally, nearly all of the traps set on a pond were cleaned of bait for a period of 4 or 5 days. Even floating sets 5 or 6 feet from shore were robbed. Field mice (*Microtus pennsylvanicus*) were almost invariably the culprits as revealed by snap-trapping checks, but jumping mice (*Zapus hudsonius*) and rats (*Rattus norvegicus*) were also snap-trapped inside live traps. The latter were captured occasionally in live traps without the aid of snap traps. Rat populations were rarely encountered except on ponds near buildings or near refuse dumps. Twenty-five species including amphibians, reptiles, birds, and mammals were captured incidentally. Information was secured from more than 700 muskrats during the study, primarily through live-trapping. Muskrat mortality due to live-trapping and handling procedures occurred in eight instances. Most of these animals were young of the year that died due to exposure to heavy rains or resultant rise in water levels. Few muskrats suffered any noticeable ill effects from their confinement in live traps.

Handling Procedures

A muskrat was removed from the live trap by quickly opening one door, grasping the animal by the tail, and forcibly pulling it out of the trap. The muskrat was then inserted into a half-cone-shaped holding device of a design similar to that described by Aldous (1946). Two pencil-sized sticks were then run through from one side of the cone to the other, immediately behind the muskrat, securing the animal tightly and enabling both hands to be used in further handling. This simple securing device was used in preference to the plunger stick described by Aldous (*loc. cit.*); tarsal and tail measurements were easily taken while the animal was held securely by the two cross-sticks, while in contrast, the plunger stick had to be removed to take these measurements.

While secured in the handling cone, the muskrat was ear-tagged, measured, sexed, aged, and examined for general condition. To insure proper placement of ear tags, the hair around the ears was clipped with scissors. A ¼-inch-long, self-piercing, numbered, monel metal tag manu-

factured by the National Tag and Band Company was placed in each ear of the muskrat with the aid of tagging pliers. Tests showed that ear tags were best inserted for only half their length into the dorsal aspect of the ear rather than to their full length. Placing tags deeply into the dorsal aspect or in fleshy parts of the ear was usually followed by minor infection, although alcohol disinfectant was used as a safeguard. The National tag (#1 size) was much more easily applied and was more efficient than the fish-fingerling type which was used briefly at the start of the study and which has been used with differing degrees of success by other investigators (Aldous, 1946; Sather, 1958). Only three tags were observed to have been lost or torn out during the entire study period of 2½ years even though young 3 or 4 weeks old were tagged. In the three instances of tag loss, one tag was still firmly attached and a definite scar was present on the other ear. Several muskrats were captured nearly 2 years after being tagged as young. They bore tags that were perfectly in place and easily read.

Measurements of the tail and left hind foot were taken with a millimeter rule while the muskrat was in the cone. The hind foot measurement was taken from the end of the nail on the center toe to the end of the heel. The tail was measured from tail tip to anal orifice since, as observed by others (Dorney and Rusch, 1953; Sather, 1958), the inflexible muskrat tail precludes the standard measurement. Total-length measurements of live-trapped adults generally were not taken because of the inaccuracy involved in obtaining a reliable measurement with live adult animals. Information on total length was obtained from young live-trapped muskrats because they were satisfactorily handled with heavy gloves. Substantial data were also secured from sacrificed animals and those taken in steel traps. Weights were usually determined by weighing the trap with the captive inside, then weighing the trap alone, using a spring scale calibrated in ounces. A simple balance was used to weigh very young muskrats to the nearest 1/10 gram. The accuracy of weighing techniques was checked frequently by reweighing the same muskrat several times during the processing procedure. Field scales were checked periodically by comparing results with more precise, nonportable scales.

Handling procedures usually had little observable effect on the muskrats. Only one death occurred and this apparently was due to heart failure, not injury.

Steel-trapping Methods

Steel-trapping was used as an accessory method to live-trapping. Water areas well removed from the study areas were steel-trapped or live-trapped or both in order to obtain additional information, especially concerning reproduction and movement, without disturbing the study areas. Steel traps were used also to check on the effectiveness of live-

trapping techniques. At the end of the study, steel-trapping was used on and in the vicinity of the study areas to expedite the collection of final data concerning movement, reproduction, and population composition. "Stop-loss" and "killer" steel trap types were used with good success.

REPRODUCTION

Data on reproduction were obtained by direct observations of wild and captive live muskrats, and by examination of nearly 250 dead muskrats. Much of the information is the result of investigations carried out on captive animals, especially during the 1959 breeding season.

MATING

Data from three breeding seasons indicated that the major onset of muskrat mating activity was closely associated with the start of spring movement periods and the favorable weather conditions that accompanied them, although a few matings are known to have occurred prior to the dates spring movement began. Earliest successful mating dates were calculated by backdating from the known or estimated birth dates of the earliest litters encountered in each of the three years. These dates were: March 2, 1957; February 18, 1958; March 6, 1959. Bednarik (1956) noted mating among muskrats in Ohio during the third week in February; other investigators mention exceptional matings in late January and early February. The initial surge in breeding activity occurred following the break up of the ice cover on the study ponds, i.e., the third week in March in 1957, the second week in April in 1958, and the first week in April in 1959, as calculated from backdated birth-date information. Aspisoff (1955) indicated that ice conditions influence the beginning of the breeding season in Russia by his statement that the start of the breeding "coincides with the appearance of open margins on the lakes". Peak periods of breeding activity took place in the latter half of April all three years. The latest known breeding dates in 1957 and 1958 were July 28 and August 7, respectively.

Seven matings were observed, four of which involved captive animals that could be closely watched. The female, in these instances, solicited the attentions of the male and, after a few minutes of scuffling, four to seven copulations lasting several seconds each took place. The female then resisted further attempts by the male. One of the captive matings involved animals that could not have encountered each other previously. Placed together for the first time, they mated following a brief period of antagonistic behavior. The two fed together after mating.

A captive female was placed with a male 2 days after giving birth to six young in an attempt to determine how soon after parturition a muskrat will breed. A mating occurred within 25 minutes. She re-

sumed nursing her young 10 minutes later. This mating was not fertile. One other such experiment 3 days after parturition yielded negative results. Olsen (1959) indicated that muskrats undergo an immediate postpartum estrus.

There is lack of agreement among investigators as to whether muskrats are monogamous, polygamous, or promiscuous. Sather (1958) indicated this but observed that his data suggest monogamy "throughout the breeding period, and even through the winter". Evidence was obtained that the muskrats I studied probably were monogamous. In at least three instances a "pair" of muskrats definitely inhabited the same burrow system or dwelling house from March through late October or into November. No other muskrats, except their offspring, were captured within these three home ranges during this period. Further evidence indicating probable monogamy was noted. Numerous pairings of at least 3 or 4 months duration were made evident by intensive live-trapping procedures during which two muskrats (male and female) were repeatedly caught in the same home range. Occasionally these animals were captured side by side on the same trap night. In two instances, a "pair" was captured in one "single-catch" live trap.

The minimum breeding age of muskrats has been considered by several investigators (Warwick, 1940; Dozier, 1953; Aspisoff, 1955; Sather, 1958). Sather alone presented data indicating precocial breeding among young of the year. The other authors suggested that young probably do not mature sufficiently to breed before the spring breeding season. In this investigation, examination of the reproductive tracts of 37 young of the year taken during October-December in 1957 and 1958 indicated that precocial breeding probably had not occurred on study area ponds or nearby ponds. Neither embryos nor placental scars were found in the tracts of these young females. This does not preclude occasional instances, but it suggests that breeding among juveniles occurs infrequently if at all, on central New York ponds.

Gestation Period

Much of the evidence concerning the length of gestation in the muskrat is based on the study of peaks in litter production. Some of it is based on approximated birth dates of successive litters born in the wild to a female kept under surveillance. Smith (1938), however, obtained experimental evidence from his study in Maryland. His experiments in 1933 with penned muskrats produced one litter of four young which was the result of a mating either 9, 19, or 29 days before birth (the days the male was with the female). A second gestation period length was indicated by one dead, newborn young that was found with a female that had been bred either 15 or 30 days previously. In summing up the information obtained from these two records, Smith stated that "it would

appear that the gestation period of the muskrat is 29 or 30 days. The other supposition possible would place it at the 15th to 19th day, a difference that is too great." He concluded by indicating that "Further information must be obtained, however, before any more definite statement can be made."

Controlled experiments were begun in the spring of 1959 in an effort to further clarify the existing information on gestation length. Six large pens, constructed of poultry netting and hardware cloth and used previously in the investigation to study the growth of young, were used to house the animals. These pens extended into the water of the fenced pond on which they were located, providing approximately 60 square feet of swimming area. The 30-inch-square nest box portion of the pen was partially filled with nesting materials and rested on dry ground. Six females, live-trapped in late March and early April, were placed in these pens and were visited daily. A male was placed with each female for a 1-day period at 15-day intervals, after she had either given birth to a litter as the result of a mating prior to capture, or after she was determined to be nongravid following a waiting period of at least 35 days. Two litters, one of six young and one of three young, were born on June 23 and June 31 as the result of mating in captivity. Neither female had bred successfully prior to being penned. One had been exposed to a male 13 and 28 days prior to parturition; the other was bred either 14 or 29 days before parturition.

Although minimal muskrat gestation lengths may possibly be as low as 22 or 23 days or even 19 days, as indicated in Errington's discussion (1937), it seems illogical to surmise that these two females had 13- and 14-day gestation periods. One captive female is known to have had a gestation period of at least 24 days since she had been penned without a male for that length of time before giving birth to a litter. A normal gestation period of approximately 28 to 30 days seems a reasonable conclusion based on the experimental data collected during this study and the only other reliable experimental records known to the author. Additional information is needed to ascertain the limits of variation within the species.

Litter Size and Number

Data on litter size, the number of litters per female per year, and the time of year these litters are born in central New York were obtained throughout the study, but the major portion of the information was collected during the last year in order to minimize disturbance of study areas.

An indication of the average litter size in 1959 was secured from eight newborn litters conceived in the wild but born in captivity, from 19 newborn to 5-day-old litters born in the wild, and from placental scar counts obtained from the reproductive tracts of 38 adult females

sacrificed during June and the first two weeks of July. All of these litters were apparently complete since no sign of disturbance was present; two that had been disturbed are not included. All captive litters were examined as newborn young; wild litters were aged using criteria established through studying the growth of newborn young in captivity.

The mean litter size of the eight litters born in captivity was 6.3 young. It was 6.1 for the 19 litters born in the wild. Placental scar counts made on the 38 reproductive tracts yielded a mean of 6.0 young per litter based on scars showing 44 distinct litters. (Six females had borne two litters as indicated by two sets of scars which were distinguishable by differences in color intensities, a criterion used by Errington, Sather and other workers.) The mean litter size for the total of 71 litters examined in 1959 was 6.2 young; the range was three to eight young.

In 1958 the mean number of young per litter was also 6.2 with a range of three to eight; in 1957 it was 6.4 with a range of three to nine. These values for 1957 and 1958 were based on a count of 81 sets of placental scars in 24 adults collected in September-November 1957 and 31 collected in September-November 1958 (26 sets represented second litters).

The samples were too small to permit critical comparison of the relative sizes of first and second litters born in each of the three years, but an indication of this was obtained by grouping the 32 females that produced two litters each in all three years. The mean litter size was 6.3 for first litters and 6.1 for second litters. These sizes, although slightly smaller, agree rather closely with those reported by Beer and Truax (1950), Errington (1951) and Sather (1958) for muskrats of the Midwest. Arata (1959) gave 3.4 young as average for muskrats inhabiting strip-mine ponds in Illinois, but he indicated that adverse environmental conditions on the strip lands may have accounted for the lower number. Dozier (1953), in considering the subspecies concerned in this study (*Ondatra zibethicus zibethicus*), stated that it "averages 6 young throughout most of its range".

In regard to the number of litters produced per year, most data have been collected on large marsh areas and may not be valid for small water bodies such as those studied here. Shanks and Arthur (1952), in one of the few papers primarily concerned with muskrats inhabiting small water bodies (mostly Missouri farm ponds), stated that "In general, we consider that a pond-dwelling female produces her first and only litter in mid-spring." Arata (1959), on the other hand, stated that on strip-mine ponds in Illinois "Two age classes of muskrats were found among the subadults in live- and steel-trapped animals, indicating that two litters a year were generally produced. The counts of placental scars seemed to substantiate this." Data obtained in this study indicate that approximately 47 per cent of the adult females that inhabit small water bodies of this region of New York State bear a second litter. This is based on

examination of 55 fresh reproductive tracts collected in September through November of 1957 and 1958. A pronounced peak in litter production was noted during the last two weeks in May in the three breeding seasons observed. No second peak was apparent. McLeod and Bondar (1952) and Olsen (1959) noted peaks approximately 28 days apart. Their records indicated a first peak in early June followed by successively smaller second and third peaks.

SEX RATIOS

Sex ratio data were obtained from 174 nestling muskrats of 29 complete litters, from 279 immature animals live-trapped in the fall, and from 375 adults live-trapped on study areas throughout most of the year. Although not nearly as extensive as some of the samples reported in the literature, the data from this rather complete sample of the study area population made possible an appraisal of sex ratio structure from day-old young through 2-year-old animals.

Palpation of the urinary papillae was used successfully for determining sex in muskrats from about 3 weeks of age through adulthood. Adults were easily separated by this method, but the papillae of newly-weaned young appeared grossly similar and had to be palpated more carefully in order to identify sex. This method was accurate from 1 week of age onward, but sexing by observing the presence of absence of teats was used from birth to nearly 3 weeks of age because it involved less effort and was accurate.

A sex ratio of 105 males to 100 females was observed in the nestlings. In the September-trapped immature animals, the ratio favored males 118 to 100. A small, known-age sample of 66 first-year adults and 19 second-year adults (Table 1) indicated a trend from a predominance of males in the spring catch to a nearly even ratio in the fall catch. This trend is shown more strikingly by month in Table 2 which lists 375 adults

TABLE 1. SEX RATIOS OF 85 FIRST- AND SECOND-YEAR ADULT MUSKRATS CAPTURED AND RECAPTURED FROM JANUARY THROUGH SEPTEMBER

Period	First-year adults			Second-year adults		
	Male	Female	Per cent male	Male	Female	Per cent male
January-March	21	9	70	8	5	62
April-June	19	16	54	6	7	46
July-September	15	18	45	4	4	50
Total	55	43	56	18	16	53

Table 2. Sex Ratios of 375 Adult Muskrats Captured and Recaptured from February through October

Period	Male	Female	Per cent male
February	17	8	68
March	35	17	67
April	104	34	75
May	78	37	68
June	72	41	64
July	27	32	46
August	24	22	52
September	38	47	45
October	21	17	55
Total	416	255	62

(234 males, 141 females) live-trapped and retrapped from February through October. These adults were not identified as to first and second year classes.

The nearly equal sex ratio found in nestlings and the unbalanced ratio favoring immature males in the fall correspond closely to the ratios reported by several investigators. These data may indicate that, as Sather (1958) suggested, "apparently an undetermined mortality factor acts primarily upon females between their birth and the winter harvest".

Beer and Truax (1950) in summarizing much of the sex and age ratio information available in the literature, pointed out that the data obtained from several studies "indicate that the adult sex ratio is different from that of the immature animals. The sex ratios in the adults were in favor of the females while in the immatures they were definitely in favor of the males." Sather (1958) indicated a change "from sex ratios favoring immature males in the first winter to an almost equal sex ratio in the second".

Sex ratio information obtained in this study appears to differ markedly from the data reported by other investigators in that the total ratio was 163 males to 100 females (416 to 255). Marked seasonal variation in trapping success may possibly have produced a bias in the February-through-June data presented here. Disregarding these "biased" months, the ratio for adults from July through October was 93 males per 100 females, which is comparable to those obtained by other workers from relatively unbiased fall and winter month data.

AGE RATIOS

Muskrats were separated easily into adult and immature classes on the basis of size, weight, and pelage until mid-October or November when many immatures closely resembled adults in these characteristics. The age determination method described by Baumgartner and Bellrose (1943), which is based on the appearance of the external genitalia, was used with good success in instances where doubt existed. Few doubtful cases were encountered as only a small number of animals was taken during late fall-winter periods.

An attempt was made to age muskrats trapped in late January and February into subadult and adult classes by the external genitalia, but it was apparent that sexual development of animals entering their first breeding season had advanced sufficiently by this time to introduce significant error.

First-year adults and adults that had undergone two or more breeding seasons were not separated. Criteria of external genitalia applied to known-age adults yielded highly inaccurate results. Although second-year adults weighed significantly more on the average than did first-year adults, weight criteria were not used because some known-age first-year adults weighed as much as known-age second-year adults (see Table 4). Pelt-primeness and zygomatic-breadth methods of age determination were not used because other considerations required the subsequent release of most captives.

The age ratio in 364 September-trapped muskrats (279 young, 85 adults) was 328 young per 100 adults, or 5.9 young per adult female. Data on reproduction indicated that adult females bore an average of 9.3 young per year on the study areas.

GROWTH

The growth of very young muskrats has been studied in detail by several investigators who developed data from rehandling wild nestling young whose ages were estimated through young known to be newborn. In this study, growth information concerning weight, total length, tail length, and left hind foot length was obtained from both captive and wild litters. The data secured from captive litters are the most complete. Nine penned, adult females each produced, and successfully nursed, one litter during the period April 30 to July 31, 1959. These litters, ranging in size from three to seven young and averaging approximately six young per litter, provided the information on growth of young in captivity reported here. Twenty-eight of the 53 young were males. Each litter was complete and known to be less than 24 hours old when first found. No protracted birth periods occurred such as the atypical 3-day birth period of a litter of "at least six" that Dorney and Rusch (1953) mentioned and that they suggested may have been caused by confinement.

Pens containing females obviously pregnant or suspected of being pregnant were checked closely during feeding operations each day to insure discovery of newborn young. Usually the presence of young in the nest was detected easily through a routine procedure involving a careful approach of the nest box and a brief listening period. Cries of the young, prompted by nervous movements of the female, were clearly audible under these conditions. Soon after discovery, newborn young were removed from the nest and taken to a nearby shelter where they were sexed, weighed to the nearest 1/10 gram, and measured (total, tail, and hind foot lengths) to the nearest millimeter. Photographs and written notations recorded the external morphological appearance. Before returning them to their nest, they were marked on the dorsal surface with merthiolate so that individuals could be identified within a litter. This mark lasted about a week at which time it was renewed with picric acid. The color was visible 6 weeks later. Removal of young from the nest was complicated by the fact that, even when touched, a female with young usually continued nursing them and remained within the nest. When prodded, she generally plunged into the edge of the nest losing some young on the way. After 2 or 3 days of age, young were able to grasp the teats more tenaciously and were seldom dislodged. It was often necessary to grasp the young by the tail and pull them forcibly from the female. Usually half the litter was removed at a time and the female continued to nurse the others. After processing the young as quickly as possible, they were returned and the others taken from her. These were processed quickly and returned. By using this approach some young were nursed throughout the whole period of disturbance, and the female rarely left the nest. When the entire litter was removed at once, the female invariably had left the nest when the young were returned. In all instances, however, the female accepted her young after handling and continued to nurse them.

Emphasis was placed on obtaining growth data at weekly intervals following birth, but some animals were observed more frequently. Weights, measurements, and notations on morphological changes were recorded for each of the first 10 days and irregularly between weekly intervals thereafter. Growth data on weight and the three linear measurements, obtained from rehandling the captive individuals from 1 through 50 days of age, are presented in Table 3. "One day of age" as used here means that the muskrat was known to be between 10 and 22 hours old when first examined. Figures 1 through 4 depict the growth curves calculated from the data presented in the table. Weights and measurements from six or more muskrats were used to obtain the actual points. A moving mean of three was used. As might be expected, correlation between the three linear measurements, weight, and age was very high throughout the first 50 days of life.

TABLE 3. WEIGHTS AND MEASUREMENTS OF NINE KNOWN AGE LITTERS OF CAPTIVE MUSKRATS FROM BIRTH TO 50 DAYS

Age in days	Number of muskrats	Mean weight (grams)	Mean total length (millimeters)	Mean tail length (millimeters)	Mean hind foot length (millimeters)
1*.....	53	23.2	102	28	15
2.....	3	26.5	111	29	17
3.....	35	29.8	125	35	19
4.....	25	34.3	134	39	22
5.....	3	42.7	145	43	23
6.....	6	40.1	146	46	24
7.....	49	46.2	150	49	26
8.....	6	50.4	160	53	29
9.....	1	61.7	172	55	29
10.....	20	58.1	168	57	32
12.....	2	69.8	184	66	35
14.....	49	73.6	191	70	38
15.....	1	87.3	203	74	38
16.....	12	79.1	195	72	40
18.....	2	94.0	209	81	45
21.....	49	117.2	234	91	49
25.....	1	138.0	235	95	49
28.....	19	161.1	264	109	54
30.....	16	173.0	275	118	55
32.....	1	169.0	281	115	54
35.....	24	196.8	300	128	58
38.....	1	227.0	302	129	58
42.....	18	238.1	329	143	62
44.....	1	256.0	328	139	61
46.....	1	252.0	364	148	64
50.....	6	270.8	383	162	65

* As used here, one day old signifies that the muskrat was between 10 and 22 hours old when first examined.

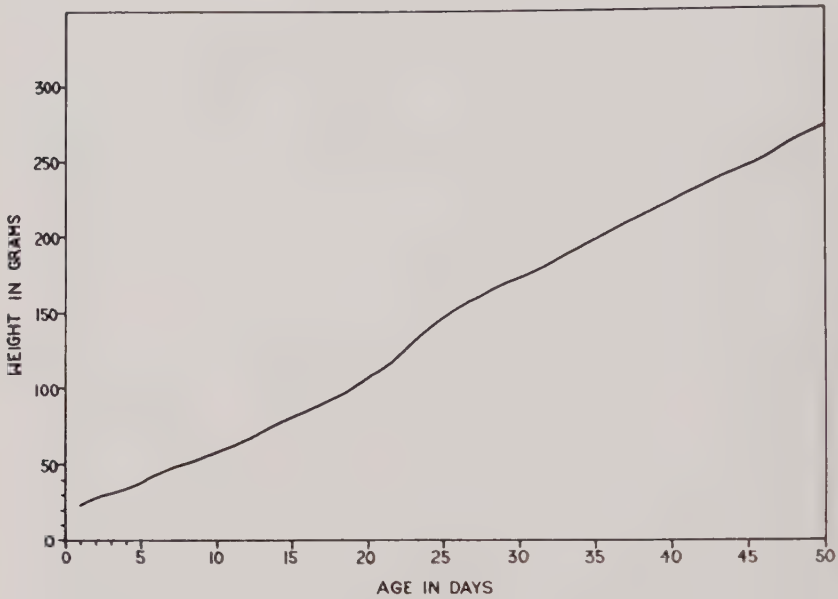

Figure 1. Weights of captive muskrats from birth to 50 days.

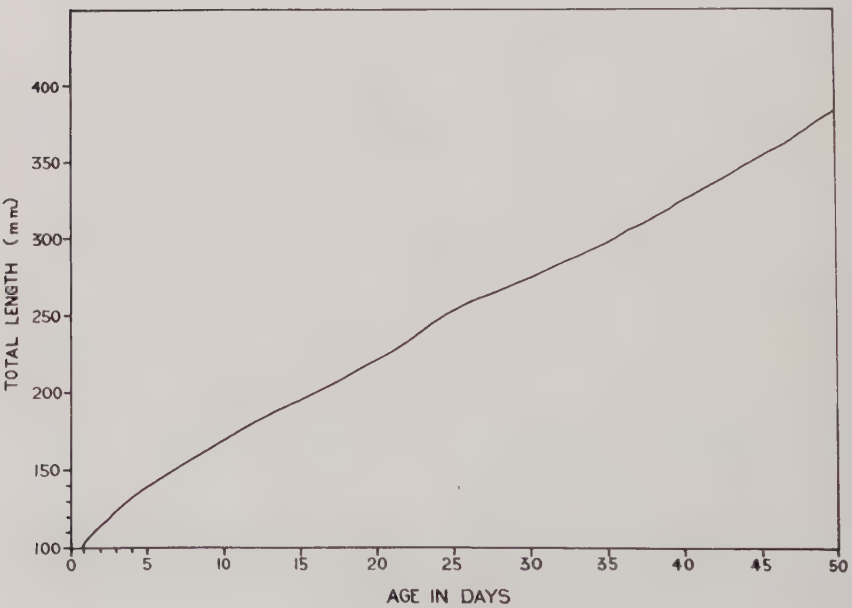

Figure 2. Total lengths of captive muskrats from birth to 50 days.

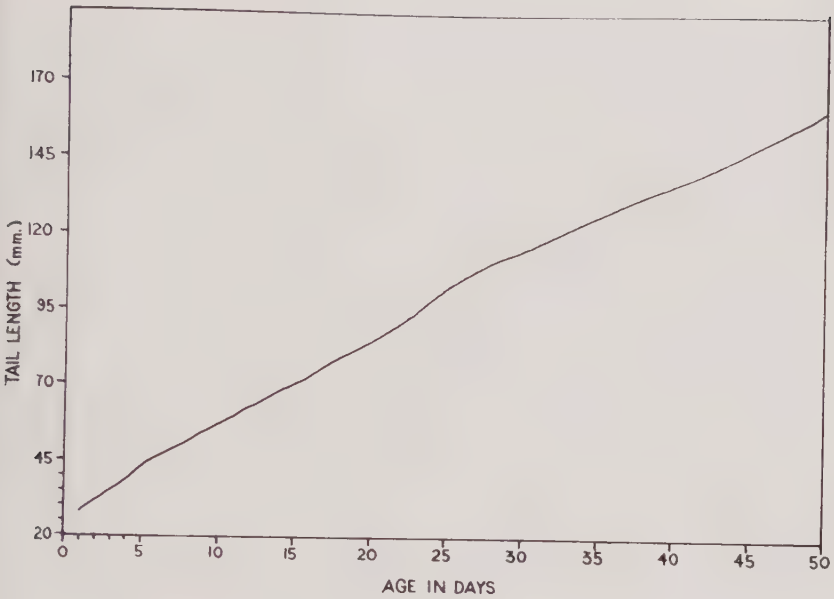

Figure 3. Tail lengths of captive muskrats from birth to 50 days.

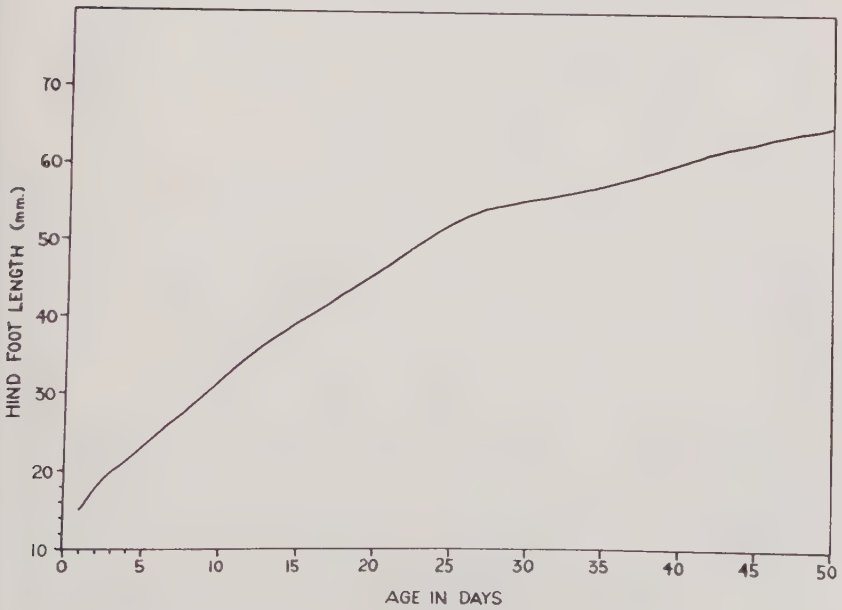

Figure 4. Hind foot lengths of captive muskrats from birth to 50 days.

Several morphological changes were especially notable for their regularity. The umbilical scab, which formed during the first day of life, usually fell off at 5 or 6 days of age; the incisors broke through the gum line at approximately 6 or 7 days of age, the lower ones usually followed by the upper ones; the eyes of nestlings opened at approximately 14 days of age; weaning occurred gradually in the third to fourth week of life.

Weights and measurements from 19 wild litters made possible a comparison of growth rates of captive and wild young. The animals, located in houses on the larger study area, were processed during the late spring of 1959. Two wild litters were judged to be day-old young, 12 were less than 1 week old and the remaining five litters ranged from 8 or 9 days of age to about 16 to 18 days. Handling and marking techniques similar to those used for captive young were employed, but some wild young were toe-clipped for identification. Unfortunately only 11 litters were reprocessed; five others were found dead in the nests, and no trace of the remaining three litters was found. Approximately 10 days had passed in each case. Care had been taken to handle litters quickly

Table 4. Weights of 85 First- and Second-year Adult Muskrats Captured and Recaptured from January through September

Period	Male			Female		
	Number	Weight in grams		Number	Weight in grams	
		Average	Range		Average	Range
First-year adults						
January-March	21	1,077	936-1,332	9	1,162	1,021-1,531
April-June	19	1,077	992-1,474	16	1,049	964-1,389
July-September	15	1,304	1,191-1,389	18	1,332	1,162-1,701
Total	55	1,153	936-1,474	43	1,181	964-1,531
Second-year adults						
January-March	8	1,389	1,247-1,474	5	1,247	1,219-1,304
April-June	6	1,304	1,219-1,418	7	1,361	1,247-1,446
July-September	4	1,418	1,332-1,474	4	1,361	1,219-1,474
Total	18	1,370	1,219-1,474	16	1,323	1,219-1,474

and houses were repaired carefully immediately after the young were replaced. Young found dead in the nest bore no wounds and were apparently deserted by the females. Three of the litters reprocessed had been moved to nearby houses. Dorney and Rusch (1953) reported similar difficulty in rehandling nestling young in the wild. Weights and measurements of wild young fell within the ranges of those of captive young of the same age. Additional information concerning growth rates of young in the wild was obtained from recapturing newly-weaned, live-trapped young that were aged, probably within 1 week of true age, when captured. These individuals were recaptured up to 2 years later and provided data on growth through two breeding seasons. Second-year adults, as a group, were much larger than first-year adults, but the two groups overlapped considerably in both weights and measurements (Table 4). Adult males generally were larger than adult females, but much overlap was evident.

An additional, more quantitative picture of growth in adults was obtained from the weights and measurements of 375 live-trapped muskrats classified simply as adult males and females. Average weights of these animals are listed in Table 5 by month. November-January weights are not reported because of insufficient data for this period. The progressive weight increase for both male and female adults from the

TABLE 5. AVERAGE MONTHLY WEIGHTS OF 375 MALE AND FEMALE ADULT MUSKRATS CAPTURED AND RECAPTURED FROM FEBRUARY THROUGH OCTOBER

Month	Male			Female		
		Weight in grams			Weight in grams	
	Number	Average	Range	Number	Average	Range
February	17	1,063	907-1,361	8	1,027	879-1,077
March	35	1,077	936-1,446	17	1,015	907-1,106
April	104	1,093	822-1,503	34	1,148	907-1,899
May	78	1,178	822-1,474	37	1,172	964-1,531
June	72	1,276	907-1,474	41	1,123	964-1,332
July	27	1,274	1,021-1,559	32	1,168	992-1,361
August	24	1,235	1,049-1,474	22	1,159	992-1,247
September	38	1,313	964-1,531	47	1,230	964-1,701
October	21	1,285	1,021-1,559	17	1,203	1,021-1,474

spring through the fall is more clearly depicted by this table. The predominance of males in the sample from February through June may possibly have been due to two factors. From February through May, males were generally more active than females as a result of differential breeding and movement activities. Secondly, most females were nursing nestling young during May-June and were less active and wide ranging than males at this time.

MOVEMENTS

The study areas were selected primarily because they afforded excellent opportunities to follow movement activities of muskrats. Movements were followed by intensive live-trapping in study ponds and along possible routes of movement such as ditches and freshets. Visual appraisal of movement signs, such as tracks, droppings, cuttings, and sightings of muskrats in locations away from normal muskrat habitat, supplemented this information. Increased frequency of road kills also was a movement indicator. Movement, as used in this paper, refers primarily to a move by a muskrat from the home pond to another pond or water area usually without subsequently returning to the pond of origin. Moves within the home pond but well outside the established home range are included also in this definition.

Fifty-seven movements involving tagged muskrats were recorded during the 2½ years of study; 39 of these were spring movements, 6 occurred during summer, and 12 in fall. In addition, 41 movements of untagged muskrats into study area ponds were noted: 22 in spring, 4 in summer, 6 in fall, and 9 probably occurring either in very late fall or early spring. Undoubtedly many movements occurred, especially during the spring periods, that were not detected by live-trapping. Trapping before and after movement periods indicated a substantially greater loss in pond populations than can be reasonably explained by known movements and natural mortality. These animals presumably moved off the study areas or were killed or died in the process of moving. Several carcasses were found well removed from muskrat habitat during the period of spring movement.

Spring Movement

Spring was by far the most active period of movement. It appeared to be triggered by the break up of ice on the ponds, resulting from several days of warm weather. Greatly increased breeding activity coincided with it. The beginning of the spring movement in 1957, 1958, and 1959 was determined by visual inspection of the study areas and by checks for highway kills. In 1958 and 1959, live traps especially insulated for winter conditions were used along possible routes of movement to augment other sources of information concerning the beginning of movement activities.

In 1957, spring movement began rather abruptly on March 15 following a pronounced spring thaw and ice break-up that resulted from three consecutive days of abnormally high temperatures. In 1958, movement started equally abruptly on April 6, the day after the break-up of ice on the ponds. Muskrats had been unusually active for the two days before movement started. In 1959, the start of the spring movement was not well defined but began sporadically and with low intensity on March 26. No significant spring thaw preceded the movement, but mean temperatures of 39.8° and 47.1° F. for 2 days prior to the start of the movement cleared study ponds of their thin layers of ice. The 1957 and 1958 spring movements both reached their peak intensities approximately 10 days after they began. The period of movement in 1957 lasted approximately 45 days. In 1958 the period was shorter by about 11 days and had virtually ceased by May 10. In 1959, the peak was reached approximately 2 weeks after movement began on March 26. The degree of movement tapered off slowly, the period lasting about 6 weeks.

Trapping data obtained before and after the spring movement period indicated that approximately 59 per cent of the muskrat population present on a study area pond prior to the movement period was still present at its conclusion. This is in rather close agreement with Aldous' (1946) findings in South Dakota which showed that "69¼ per cent of the recatch records indicate no migratory movements". As can be seen in Table 6, most spring movements of tagged individuals covered relatively short distances, but it should be mentioned that long moves would be more likely to carry the muskrat off the study area thus making recapture, less likely than if shorter moves were made. To minimize the effect of this variable, water areas on the periphery of the study areas were trapped periodically, especially following movement periods.

The mean distance for muskrat travel during the three springs for which data were collected was 734 feet. The longest movement was nearly a mile. Almost all movement was from pond to pond. Four significant spring movements within marshes (movements well outside an established home range) were detected on the two largest small marshes studied during 1958 and 1959. These movements are indicated in Table 6. There was no evident pattern of movement as to compass direction during spring, summer or fall periods. Movements took place most often from ponds of higher elevation to ones at lower levels. This was especially evident during wet weather when muskrats tended to follow freshets downhill. Movements occurred from nearly all study ponds, and no correlation could be established between the size of a pond, its condition, or its muskrat population density and the extent of loss through movements during this period. A sex differential decidedly favoring males (nearly 3 to 1) was present in the spring movement as indicated by the tagged individuals listed. These observations are somewhat sub-

Table 6. Spring Movements of 39 Muskrats in Central New York Ponds in 1957, 1958 and 1959

Year	Movement number	Distance in feet	Sex	Age *
1957 §	1	1,000	male	..
	2	275	male	..
	3	275	male	..
1958	4	200	male	1
	5	1,700	male	1
	6	1,300	female	1
	7	450	male	..
	8	400	male	..
	9	375	male	..
	10	425	male	..
	11	525	male	1
	12	250	female	..
	13	525	female	2
	14	300	male	2
	15	325	male	..
	16	575	male	1
	17	1,000	male	1
	18	1,300	female	2
	19	825	male	1
	20	625	female	1
	21	350	female	2
1959	22	825	female	1
	23	775	male	1
	24	825	male	2
	25	575	male	1
	26	575	male	2
	27	275	female	1
	28	550	male	..
	29	1,400	male	2
	30	825	male	1
	31	5,000	male	1
	32	700	male	1
	33	250	female	..
	34	275	male	1
	35	1,500	male	..
	36†	325	male	1
	37†	275	female	2
	38†	375	male	1
	39†	425	male	..

* First or second breeding season.

§ Live-trapping procedures were just getting under way in the spring of 1957; this possibly accounts for the relatively small number of movements of tagged muskrats detected during this season as compared with those of 1958 and 1959.

† These movements were restricted to one water area; all others occurred between two.

stantiated by the fact that 14 road-killed muskrats, which were definitely on the move, were examined during the spring period and only five were females.

Close attention was given the question of precisely what causes and initiates the spring movement. After consideration of all the factors pos-

sibly involved, it appeared evident that ameliorating snow and ice conditions combined with warm weather were of prime importance in triggering this behavior, markedly so in 1957 and 1958, and to a lesser extent in 1959. Break up of pond ice preceded by at least several days of abnormally high maximum temperatures and near or above freezing mean temperatures occurred before the beginning of the movements reported. Although apparently triggered by the break-up of ice on the ponds, accompanied by warmer weather, the "increased irritability of the animals" and "urge within the animal to move", referred to by Beer and Meyer (1951), appear to hold the answer as to the underlying cause of the movement.

Signs of increasing restlessness were noted in late February and March each year, especially after abnormally warm nights, and the increasing number of freshly scarred animals appearing in the catch throughout this same period attested to a mounting intraspecific friction or irritability within the population. Presumably the animals are readied physiologically for breeding and psychologically for moving. It is theorized that the occurrence of a pronounced thaw and ice break-up at this time will abruptly trigger movements (as in 1957 and 1958) and that a gradual thaw will result in a less obvious start of movement during perhaps two or three warm days when water areas are nearly free of ice (as in 1959).

SUMMER AND FALL MOVEMENTS

Summer and fall movements occurred at a much lower intensity than spring movements, and individual movements averaged less distance. Only six summer movements of tagged muskrats and four of untagged ones were detected during the study although intensive live-trapping was conducted throughout the summers of 1957 and 1958, and the early part of the summer of 1959, in part to assess this phase of movement activity. The six tagged individuals (Table 7) taken during the three summer months traveled relatively short distances compared with the mean distance for spring movements.

The fall movement, although rather low in intensity compared with the spring movement, appeared to cover nearly as long a period of time. No exact beginning or ending dates were assigned due to the difficulty encountered in following the relatively small number of muskrats apparently involved. Peaks of activity were correlated rather closely with periods when water was flowing in ditches and freshets and when temperatures were abnormally high. Eighteen fall movements were detected through live-trapping; 12 involved previously tagged individuals that moved a mean distance of 481 feet (Table 8). In addition, five road kills were examined that were judged to have been moving individuals because of the distance from any habitable water area. Of the 23 fall migrants examined, 13 were females and 10 were males; 15 were

Table 7. Summer Movements of Six Muskrats in Central New York Ponds in 1957 and 1958

Year	Movement number	Distance in feet	Sex	Age
1957	1	350	male	adult
1958	2	350	female	young
	3	325	male	adult
	4	375	female	adult
	5	475	female	adult
	6	325	male	adult

Table 8. Fall Movements of 12 Muskrats in Central New York Ponds in 1957 and 1958

Year	Movement number	Distance in feet	Sex	Age
1957	1	325	female	young
	2	500	female	adult
	3	350	male	adult
	4	300	female	young
	5	400	female	adult
1958	6	350	female	young
	7	375	male	adult
	8	375	male	young
	9	450	male	young
	10	350	female	adult
	11	1,600	male	young
	12	400	female	young

subadults and 8 were adults. As mentioned previously in connection with movement in general, many more muskrats moved than were detected. Calculations based on live-trapping pond populations before and at the close of fall movement indicate that approximately 25 per cent of a pond population is lost to this activity. Egress was considerably

greater than ingress at this time, a fact observed in this study in connection with all movement periods. Shanks and Arthur (1952) reported a greater loss (45 per cent) due to the "fall shuffle" in Missouri farm ponds and streams, but they indicated similar findings in regard to the egress-ingress ratio in general. Data suggested that intraspecific strife is associated with fall movement. No precise causes were apparent to explain summer movement.

HOME RANGE

Summer home ranges of adults were studied on an 8-acre small marsh in 1958. Intensive live-trapping was used to assess the home-range structure of the adult population. Prior to June, numbered stakes were placed at 50-foot intervals around the perimeter of the pond, on natural elevations within the marsh, on muskrat houses, and on feeding platforms. This made possible accurate plotting of trap sites and points of capture. Periodically from June through August, live traps were stationed at intervals of approximately 25 feet on the most advantageous sites around the perimeter, and on the stations within the marsh. Usually, traps were

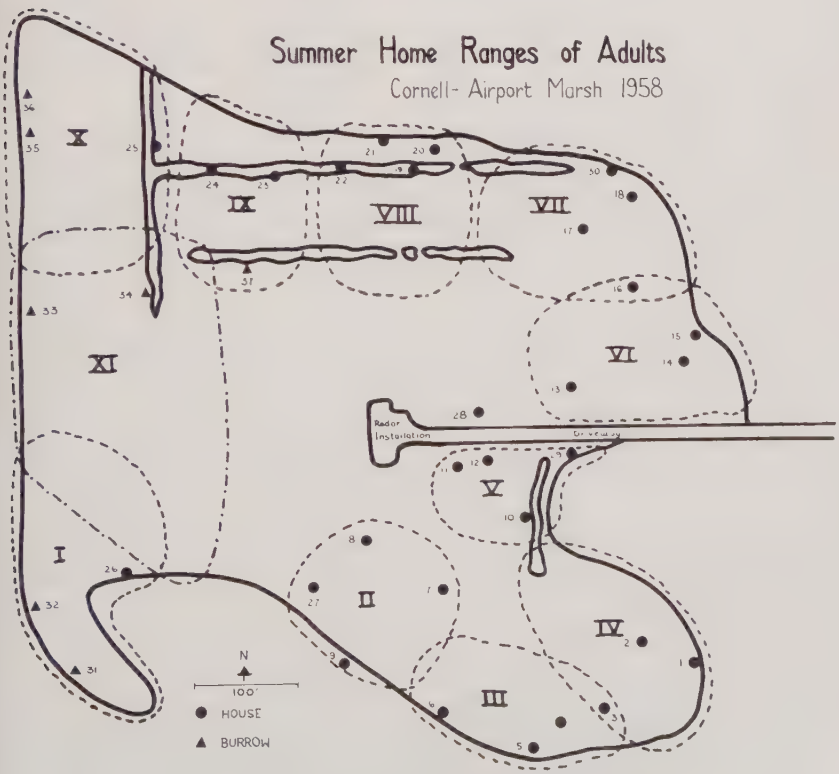

Figure 5. Summer home ranges of 21 adult muskrats.

left at one site from 3 to 6 days and then moved. If an animal was caught in the same set on two consecutive days the trap was moved and not replaced for approximately 2 weeks. Twenty-one adults were present on the marsh during the 3-month period of study. No special effort was made to assess the young present in the population, but 27 were captured incidentally while determining home ranges of adults.

Home ranges of 10 adult males coincided with those of 10 adult females to such an extent that pairing was indicated (Figure 5). Both members of these "pairs" were often captured on the same dwellings and feeding stations, sometimes side by side. One adult male apparently

Table 9. Homing Data for 11 Muskrats Released Along Roadsides Away from Home Ponds

Muskrat No.	Age and sex	Release point		Date released	Days until recaptured *	Homing
		Distance in feet	Direction			
109.....	Ad. male	3,600	NE	April 24	3	yes
		5,900	N	April 28	..	no
58.....	Ad. male	3,300	N	April 24	32	yes
		2,500	W	May 26	..	no
332.....	Ad. male	3,100	E	April 5	2	yes
		2,700	S	April 7	..	no
629.....	Ad. male	3,300	N	April 22	17	yes
		2,700	S	May 10	12	yes
		3,100	E	May 23	2	yes
		3,500	W	May 26	22	yes
		4,800	NE	June 19	1	yes
		7,600	N	June 20	..	no
526.....	Ad. male	3,300	E	October 13	1	yes
		3,500	SW	October 14	4	yes
		3,100	E	October 18	..	no
644.....	Ad. female	3,300	N	April 22	..	no
12.....	Ad. female	2,700	W	August 27	..	no
320.....	Ad. female	3,100	E	April 5	..	no
333.....	Im. male...	3,300	N	October 13	1	yes
		3,700	NW	October 14	..	no
329.....	Im. male...	3,100	E	October 13	1	yes
		3,500	NE	October 14	..	no
536.....	Im. female	3,100	E	October 29	..	no

* In some cases, because of inclement weather, a muskrat was not released until the day after it was captured. Although traps were visited and the animals processed in the morning, the muskrats were not released until late evening to avoid undue predation that probably would have occurred during daylight hours.

remained unmated during the period. His home range (number 11) was larger than the home ranges of the 10 "paired" adults and overlapped several of them. Home ranges averaged approximately 200 feet in diameter. Slight overlap occurred between the ranges of several "paired" adults. Weaned young lived within the confines of the parental home range, but often they left the main dwelling in late summer and moved short distances to rebuilt or newly constructed dwellings. No indications of intraspecific strife were noted on this marsh during the summer of 1958. No detailed study was made of home ranges during fall, winter or spring months. Different individuals were, however, caught more frequently at the same trap site during these periods, possibly indicating a greater overlap of their ranges then. Data obtained definitely indicate that muskrats range most widely during fall and spring months.

HOMING

No specific studies of homing tendency in muskrats were located in the literature. Such information would have practical application since muskrats are a growing problem in farm ponds and other artificial impoundments, and often must be removed to avoid serious burrowing damage to dikes and other pond banks. Some owners prefer to catch muskrats alive and release them some distance from their pond, hoping they will find a new "home" and not return. The release point usually is located along a road, at most a mile or two distant from the home pond. Other pond owners transport the animals to another water area, usually nearby, hoping they will remain there. Several times I have been queried as to how far muskrats need to be removed to be certain they will not return to their home pond. Limited tests were made during this study, partly to answer this question, but primarily to learn if a homing tendency were present generally in muskrats, and in what degree.

Homing data were obtained from 19 ear-tagged, immature and adult muskrats released one or more times at varying distances and directions from home ponds. Some animals were released on other ponds, others along roadsides. Eleven of the 19 muskrats returned once. One adult male returned five times. He was released at sites located north, east, south, west and northwest of his home pond. On the fifth occasion, he returned 4,800 feet overnight from a roadside release point. An immature female returned over one mile (5,400 feet), the longest homing distance detected.

Information obtained from releasing the 19 individuals a total of 36 times is shown in Tables 9 and 10.

Detailed examination of data revealed that muskrats had returned uphill, downhill, through woods, over small intermittent streams, past other ponds, and during clear, cloudy, and rainy weather. They returned from pond and roadside release sites located in all directions from

Table 10. Homing Data for Eight Muskrats Released on Ponds Away from Home Ponds

Muskrat No.	Age and sex	Release point		Date released	Days until recaptured	Homing
		Distance in feet	Direction			
451.....	Ad. male	5,100	NW	July 16	..	no
457.....	Ad. male	5,100	NW	July 17	..	no
426.....	Im. male	600	NW	July 15	1	yes
		1,100	W	July 16	7	yes
		5,100	SW	July 24	..	no
428.....	Im. male	500	NE	July 16	2	yes
		1,100	W	July 18	..	no
452.....	Im. male	1,200	W	July 17	..	no
435.....	Im. female	1,200	W	July 16	..	no
464.....	Im. female	500	NE	July 20	5	yes
		1,000	W	July 26	30	yes
		5,100	NW	August 28	..	no
529.....	Im. female	5,400	S	August 25	54	yes *

* Not released again for homing due to cold weather.

home ponds. Muskrats that failed to return to their home ponds were not subsequently recaptured on other study ponds. This suggests extensive loss due to predation or to other causes, but no evidence was uncovered to support this supposition.

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TUBERCULOSIS IN A WILD WHITE-TAILED DEER[1]

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ABSTRACT

Bovine tuberculosis was demonstrated in a white-tailed deer killed by a hunter in Delaware County (N.Y.) during the 1961 open season. *Mycobacterium bovis* was isolated by guinea pig inoculation. The appearance of the lesions is illustrated. Although this disease is rare in wild deer, two other cases were reported in 1934 from the same general locality. Both cattle and deer populations are high and a continuing low incidence of tuberculosis is present in cattle in this area.

Tuberculosis in wild mammals is rarely recorded.[2] This paper documents infection in a wild white-tailed deer (*Odocoileus virginianus*) by the bovine strain of tuberculosis (*Mycobacterium bovis*). The gross lesions are described. It also discusses the possible role cattle may play in infecting deer. It is hoped that the information will aid wildlife workers in watching for and recognizing this disease.

POST MORTEM FINDINGS

On November 25, 1961, a 5½-year-old female white-tailed deer, killed by a hunter near Walton in Delaware County, was submitted to the project leader for examination. The deer had been field dressed by the hunter. The lungs had been left intact, the stomach and intestinal tract removed and the liver replaced in the body cavity.

Examination showed multiple abscesses, 2 to 20 millimeters in diameter, which contained light grayish yellow caseous or granular pus. These abscesses were scattered throughout the lungs, mediastinum, pulmonary pleura, parietal pleura, and diaphragm (Figures 1 and 2). Some mediastinal lymph glands were slightly enlarged. The liver appeared normal.

Acid-fast organisms suggestive of tubercle bacilli were observed in films prepared from pustular material stained by the Ziehl-Neelsen method, and in sections of lesions from the lung and diaphragm stained with Ziehl-Neelsen and hematoxylin-eosin stains. Infiltration of phagocytic cells, Langhans' giant cells, caseation, and calcification (Figures 3, 4 and 5) were noted in tubercles examined microscopically.

Direct primary isolation of bacteria on artificial media was unsuccessful. However, typical lesions were found on necropsy in the lungs, liver,

[1] A contribution of Federal Aid in Fish and Wildlife Restoration Project W-35-R. The authors wish to acknowledge the helpful advice of Dr. Donald Dean and Dr. George Baer in connection with the preparation of this paper.

[2] Not including captive wild animals.

Figure 1. Gross appearance of tubercular nodules in a white-tailed deer infected with tuberculosis showing lesions in the lung (a) and on the pleura (b).

spleen and lymph nodes of a laboratory guinea pig 60 days following intramuscular inoculation with 1 milliliter of sodium hydroxide-digested deer lung tissue.

Tissue from this guinea pig, digested with sodium hydroxide, inoculated on Lowenstein-Jensen medium without glycerol and incubated for 30 days at 37° C., yielded good growth of flat, small, translucent colonies suggestive of the bovine strain of *Mycobacterium*. When representative colonies of this microorganism were inoculated in Dubos-Davis broth without Tween 80, "serpentine cords" characteristic of the mammalian acid-fast bacillus (Smith and Conant, 1960) were noted. Colonies on a Dubos-Davis agar plate were microscopically typical of the mammalian strain of *Mycobacterium* (Gruft, 1962).

The micro-niacin test was negative, thus differentiating this culture from the human tubercle bacillus (Tarshis, 1961). The catalase test at 68° C. and pH 7 was negative; this test differentiates the human and bovine strains from all other mycobacteria (Kubica, 1960). Further, a laboratory rabbit necropsied 86 days following intraperitoneal inoculation with a 1-milliliter suspension of the bacillus revealed generalized

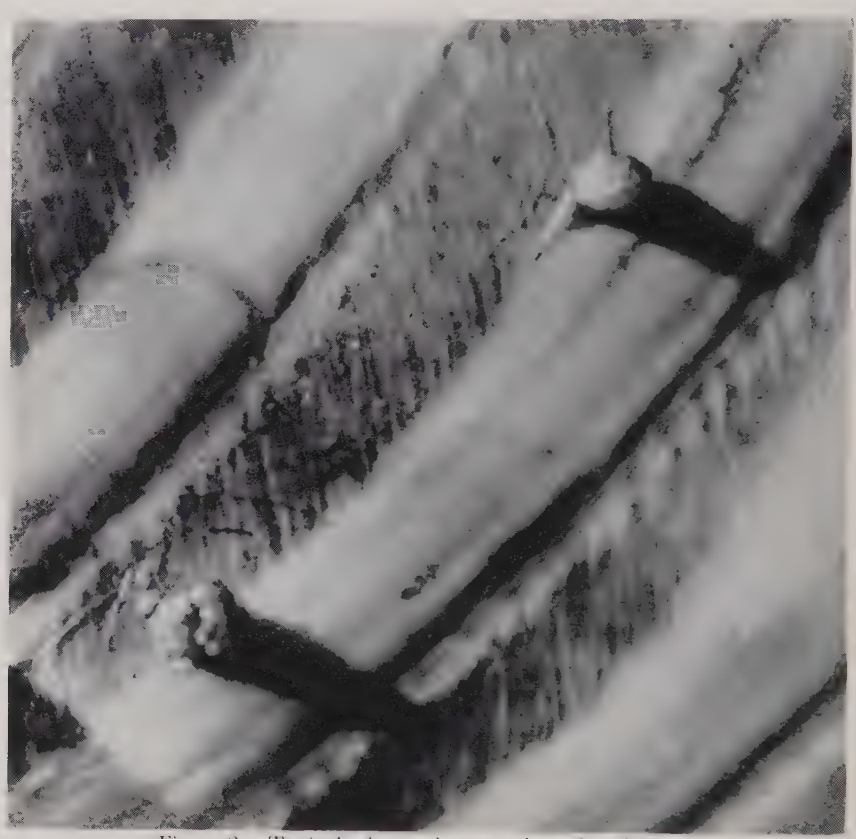

Figure 2. Typical advanced-stage tuberculous lesions.

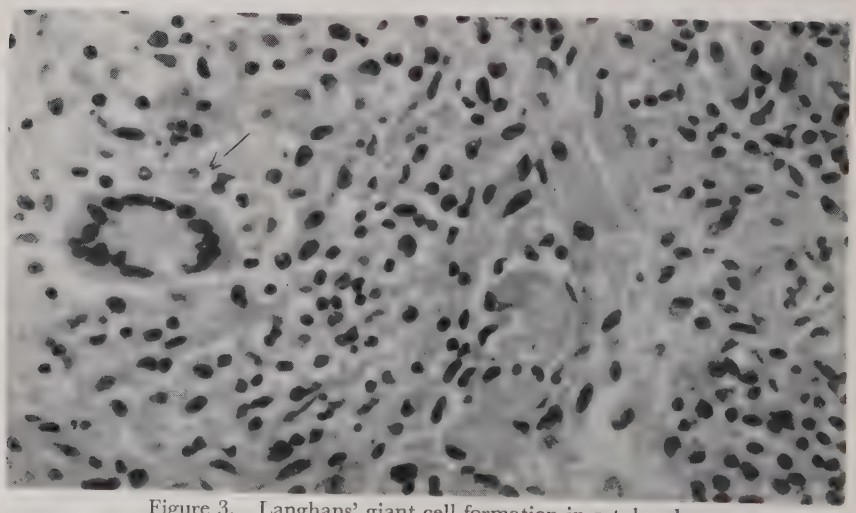

Figure 3. Langhans' giant cell formation in a tubercle.

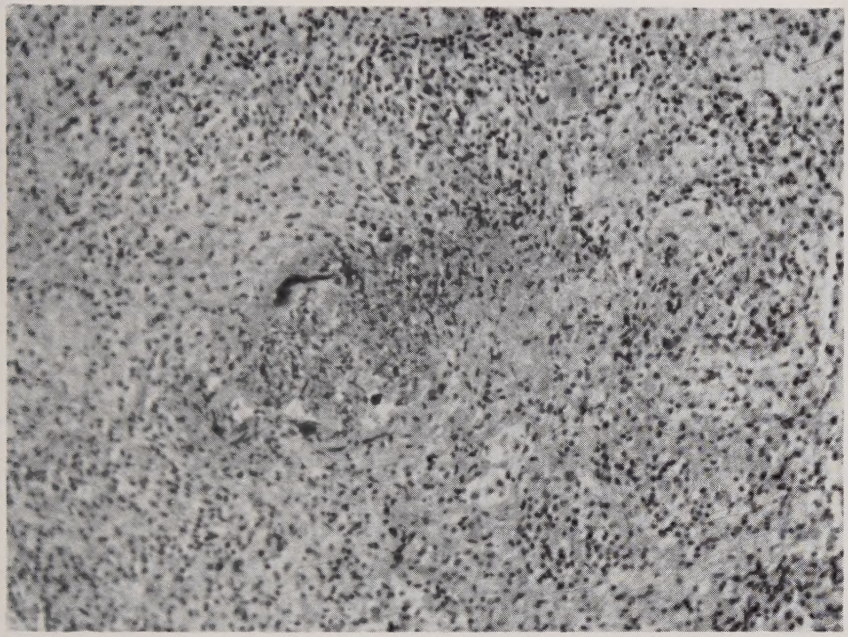

Figure 4. Microscopic section showing early tubercle formation and mass infiltration of phagocytic cells.

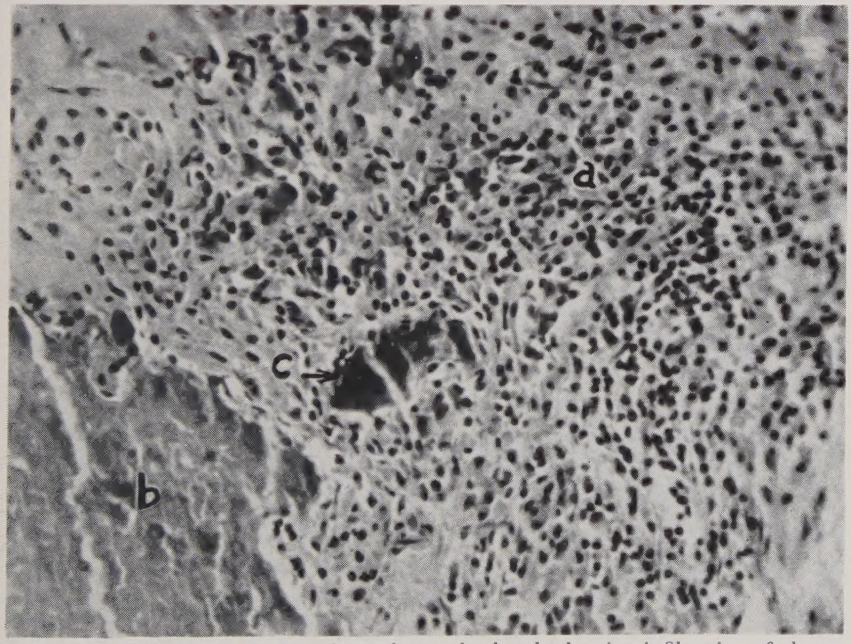

Figure 5. Microscopic section of an advanced tubercle showing infiltration of phagocytic cells (a), caseation (b) and calcification (c).

tuberculosis with marked emaciation, greatly enlarged inguinal lymph nodes containing caseous pus, and many gray nodules (tubercles) 1 to 5 millimeters in diameter scattered throughout the lungs and kidneys. The spleen contained several small (1-2 millimeter) abscesses. Films made from infected organs contained acid-fast bacilli. These findings indicate that the isolate was *Mycobacterium bovis*.

DISCUSSION

Tuberculosis in wild white-tailed deer has been reported on only four previous occasions; twice by Levine (1934) and once by LeDune (1937) in New York State, and once by Belli in Canada (1962). Between 1923 and 1940 Hadwen (1942) found bovine tuberculosis in two (0.8 per cent) of 242 mule deer (*Odocoileus hemionus*), six (5.6 per cent) of 107 moose (*Alces alces*), 73 (5.5 per cent) of 1,329 elk (*Cervus canadensis*) and 6,450 (53.73 per cent) of 12,005 bison (*Bison bison*) in the herds of the National Buffalo Park of Canada.

Tuberculosis in wild ungulates has in some instances been associated with infection in domestic cattle. In this connection Fox (1923) and earlier workers were aware of the importance and possible interrelationship of tuberculosis in domestic and captive animals. Paine and Martinaglia (1929), who reported tuberculosis in kudu (*Strepsiceros strepsiceros*) and a cape duiker (*Sylvicarpus grimmi*) in South Africa, attributed infection to contamination of water holes by domestic cattle during a period of severe drought.

The importance of the role, if any, deer may play in the continued transmission of tuberculosis to domestic livestock is unknown as is the source of infection in deer although cattle are suspect. Kurtze (1961) indicated that wild red deer (*Cervus elaphus*) served as a reservoir of infection for cattle in Germany; he believed transmission was accomplished both by direct contact and through contamination of the pasture. He also documented deer to deer transmission in wild animals. Notwithstanding Kurtze's findings, evidence suggests that cross infection between wild deer and cattle is rare and usually occurs from cattle to deer. Griffith (1928) and Scott (1930) believed that tuberculosis did not exist in wild animals living in a truly wild state.

Little is known about signs of infection in deer with tuberculosis. Francis (1958, p. 244) reported underdevelopment of the antlers as a characteristic feature and indicated that condition of the antlers in male animals may be indicative of the degree of infection in a herd. Other signs included sluggishness and a tendency for seclusion and sexual indifference in stags. It is not known, however, whether he was referring to red deer or to roe deer (*Capreolus capreolus*). Other diseases may cause similar signs. Moreover, poor range and low nutritional quality of

available food have been reported by French *et al.* (1955) and Severinghaus *et al.* (1950) to cause poor antler development.

It is noteworthy that the two cases of tuberculosis reported by Levine (1934) were from the same general area as this case; one case was from the same township. Delaware County is the third ranking dairy county in the State. Tuberculosis is present in cattle although the incidence is low. Deer are also plentiful and heavily hunted. A large dairy cattle and deer population favors transmission of infection from cattle to deer and intensive hunting favors recovery of infected deer. This may be one reason that all reported cases of tuberculosis in deer in the State have been from this area.

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